Systematic Zoology

SOCIETY OF SYSTEMATIC ZOOLOGY

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VOLUME 10 DECEMBER 1961 NUMBER 4

Systematic Zoology

LIBBIE H. HYMAN, *Editor*

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SYSTEMATIC ZOOLOGY is published quarterly, on or about the tenth day of March, June, September, and December, by the Society of Systematic Zoology. Manuscripts and correspondence about the contents of the journal and other editorial matters should be addressed to the editor, Dr. Libbie H. Hyman, American Museum of Natural History, New York 24, New York.

Subscription rates are $4.00 to members, $6.00 to non-members and institutions. The price of single numbers when available is $2.00. Back volumes are available at the rate of $8.00 per volume when in stock. Annual dues are $2.00. Correspondence regarding subscriptions, purchases, non-receipt and all other non-editorial business should be addressed to the Business Manager, Dr. Jay M. Savage, Department of Biology, University of Southern California, Los Angeles 7, California. Correspondence concerning membership and other aspects of the Society's affairs should be addressed to the Secretary, Dr. R. Tucker Abbott, Academy of Natural Sciences, Philadelphia 3, Pennsylvania.

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THE SOCIETY OF SYSTEMATIC ZOOLOGY

Systematic Zoology

VOLUME 10, 1961

NUMBERS 1–4

ISSUED 1961, BALTIMORE, MD., U. S. A.

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PUBLISHED BY

THE SOCIETY OF SYSTEMATIC ZOOLOGY

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Symposium: The Philosophical Basis of Systematics

THIS SYMPOSIUM of the Pacific Section of the Society of Systematic Zoology was held June 22, 1961, at the University of California at Davis, California. Paul R. Ehrlich of Stanford University acted as Moderator, and gave a short introductory paper. Only four of the seven papers of the symposium are presented here; others may follow in a later issue of the journal.

Systematics in 1970: Some Unpopular Predictions

PAUL R. EHRLICH

IF MENDEL were to be reincarnated in a modern genetics laboratory he would be surrounded by an array of unfamiliar equipment. Perhaps a phase contrast microscope or an amino acid analyser would confront him, or he might find himself staring at myriad bottles imprisoning tiny flies. If the clatter of a compressor or the hum of an ultracentrifuge did not disconcert him, then the talk of the geneticists surely would. His ears would be assaulted by a gibberish of DNA, mutagens, inversions, transductions, *Neurospora*, diakinesis, confidence intervals, stable equilibria, information theory, and the like.

In contrast, if Linnaeus were to materialize in the laboratory of a modern museum taxonomist, he would probably feel right at home. The collections might be larger and better curated, but they would, unmistakably, be collections. The taxonomist would be busily doing just what Linnaeus used to do—arranging organisms into groups which appeared to be homogeneous, naming these groups, and deciding where in a classificatory hierarchy the groups belonged. It would be only when the taxonomist *explained* what he was doing that Linnaeus would begin to feel uninformed—he would hear about arranging organisms in line with evolutionary trends, recent common ancestors, and such. However, as soon as he had learned to discourse in modern evolutionary patter, Linnaeus could go right back to work, for the actual procedures of taxonomy have, indeed, changed very little in the last 200 years.

Happily this period of stasis is coming to an end. I think that there will be a greater difference between the taxonomy of 1958 and the taxonomy of 1970 than between the taxonomy of 1758 and that of 1958. Having made this somewhat heterodox statement, let me confirm myself as a heretic by making some predictions about systematics in 1970.

In 1970 electronic data-processing equipment will be the most important tool of the taxonomist. Techniques will have been devised which will permit, with the aid of this equipment, repeatable and relatively exact assaying of systematic relationships.

There will be rather drastic changes in

our system of nomenclature. Emphasis will have shifted away strongly from the naming of different kinds of organisms towards the description of the interactions among them. The inadequacy of *any* nomenclatorial system for the task of describing organic diversity will be widely recognized, and binomens will be considered merely convenient landmarks in the continuum of life. Names in general will be considered analogous to floats thrown in the ocean to be used in charting currents. Too many floats would confuse the picture, too few would lose detail. The names of the people who helped to push them into the water would have no significance.

Long pseudolegal arguments over such vital matters as whether the spider wasps should be called Pompilidae or Psammocharidae will become less and less common as names are de-emphasized, and the need for international nomenclature commissions will fade.

The literature itself will take on a new character. Taxonomic monographs will be less cumbersome as the lengthy synonymies, masses of unanalysed data, and lists of type material become unacceptable for publication. Relationships will be presented in condensed form, either as a matrix of coefficients measuring similarity, or as a dendrogram expressing the structure of such a matrix. Raw data will be made available, on request, in a form suitable for computer handling.

Large general collections will retain value as records of the diversity of life, but their value in scientific research, already much decreased, will become nil. It is already apparent that the worker on evolutionary problems must, in most cases, do his own sampling, suited to his own special problem. The use of large numbers of characters will greatly diminish the usefulness of holotypes, and other type material will no longer be designated. The general inefficiency, indeed almost total uselessness, of continuing madly to collect and describe briefly multitudes of new insects, mites, nematodes, protozoa, and the like will be widely recognized. We have long since reached a plateau at which such activity largely results in the uncovering of occasional curiosities rather than in the furthering of our understanding of the world of life. Those who argue that it is necessary to name every living organism in order to "finish the job" ignore the necessity for using judicious sampling in our efforts to understand the universe. They might just as well argue that it is necessary to measure and name every grain of sand in order to understand a beach.

The shift to a more rigorous methodology may well lead to a restoration of significant feedback of ideas from taxonomy to other biological disciplines. Areas which seem ripe for this are, in particular, development and population genetics. The study of development, now in a very mechanistic, non-comparative stage, may be ready in 1970 to employ the comparative methodology being developed in taxonomy. Studies of the phenetic relationships of different stages in the life cycles of the same organisms may help to answer some of the important questions of the relative roles in ontogeny of the genetic information and its milieu. Similarly, population genetics, in trying to generalize its results from studies of single loci to the entire genome, may also find estimates of total genetic similarity useful.

So much for the crystal ball, cracked or clouded as it may be. Many of the topics touched on here will be dealt with in detail by other participants in this symposium. I trust that they will not all agree, either with me or with each other.

The Development of an Operational Approach in Plant Taxonomy

NORMAN H. RUSSELL

PARTICULARLY within the last decade, though occasionally before this for 100 years or more, voices have been raised in protest against some of the postulates and involvements of Linnaean taxonomy. Though these arguments have been primarily philosophical—stating in various ways that the species concept and the hierarchical arrangement of categories are subjective and illogical—they have become more practical today. The system is becoming increasingly burdened. Perhaps 350,000 species of plants have been described. Each has been named, on the average, several times. The descriptions of many of them, originally brief morphological sketches, are being increased with cytological, genetic, chemical, ecological, and other types of data. Reshuffling of names and even categorical assignments increase as the number of taxonomists and the amount of work they do increase. Trying to keep order in this impending chaos taxonomists follow a set of rigid, conservative rules which change less and less as our knowledge of plants grows greater and greater. The working taxonomist–the monographer–finds himself now called upon to make hundreds or thousands of decisions regarding characteristics to be studied, sampling techniques, proper statistical treatments of data, assignment to categories, etc. Nearly all of these are "intuitive" or "value" judgments. He must choose certain characters, certain sampling techniques, etc., and he has many of each to choose from. What guides him in his choices?

In the time of Linnaeus it was the so-called "constancy" of characteristics–as, in a way, it still is for most taxonomists. In defining a class of objects such as *Quercus alba* L., the white oak, the taxonomist attempts to find characteristics among the individuals studied which are the same or nearly the same in all the individuals, avoiding those characteristics which vary widely from plant to plant. For this reason Linnaeus and virtually all his successors have been predominantly concerned with certain reproductive features, such as the number and arrangement of the stamens and the parts of the pistil.

Today we have more sophisticated methods of study, but I believe that we still continue to stress similarities and avoid differences, even in such modern studies as those upon chromosome number, pigmentation, physiological reactions, etc.

What is a rational explanation for this approach? In the time of Linnaeus and nearly until that of Darwin, 100 years ago, it was commonly believed that God had created separately kinds or species of living things upon the earth—that though we could not avoid seeing overlap among them, this overlap had been derived subsequently to their creation. It was therefore believed that each species could be found and identified by a thorough search: its original core of characteristics could be reconstructed. The species originally was an idea in the mind of God. This philosophical approach—as has often been pointed out—can be traced to Aristotle, thence to Plato, and presumably backwards in history to early man when verbal communication was first developed. At least we find that our most primitive savage tribes today have it.

Darwin and Wallace, particularly Darwin, apparently upset the applecart, indicating with the theory of evolution by natural selection that species were far from immutable, that they were transient occurrences, always changing, and perhaps not real things at all but only definitions, useful but unreal classes. Like the electron, their mass, position, and movement could not be defined simultaneously. What might this do to the species concept—the one basic category of taxonomy? Did it not render the question "do species exist?" completely meaningless? Darwin apparently thought that it did for in the conclusion to his *Origin of Species* (1859) he said:

> "Hereafter we shall be compelled to acknowledge that the only distinction between species and well-marked varieties is, that the latter are known, or believed to be connected at the present day by intermediate gradations, whereas species were formerly thus connected. Hence, without rejecting the consideration of the present existence of intermediate gradations between any two forms, we shall be led to weigh more carefully and to value higher the actual amount of difference between them. It is quite possible that forms now generally acknowledged to be merely varieties may hereafter be thought worthy of specific names; and in this scientific and common language will come into accordance. In short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect; but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species."

I am sure you must all believe that up to this point I have treated taxonomy unfairly. Certainly, as many modern taxonomists have stated, we have discarded the old typological species concept and the belief in the absolute realness of our categories and classes, in the light of evolution theory. We have recently become interested in populations instead of individuals, in variable characteristics and mathematical methods of analyzing this variability, in change instead of constancy. Our species definitions now must take into account a sampling of the individuals of the species and the variability among them. We do not neglect any observable features. We consider the element of change and have attempted to bring this into our taxonomic system. We have truly profited by evolution theory and have a more natural, real, and objective taxonomy. But, indeed, have we accomplished all this? It appears that we have not. Instead of discarding our futile searches for species, as Darwin suggested we should, we have reinforced them. Our typological thinking has not been replaced at all. By using the catchwords and phrases of Darwin we have cleverly hidden it. Can this be true?

Today we define individual organisms by series of measurements or size classes and by series of less easily definable classes of qualities. We are now attempting to represent qualities numerically. For example, instead of describing petals as red, yellow, or blue, we can determine, through chromatographic techniques, the precise pigments involved and their relative amounts. This enables us to express the characteristics of the organism more precisely—that is, to define our sense impressions more accurately. In the definition and communication of some of our sense impressions we are improving. I say "some" because we continue to choose particular observable features of plants and animals for detailed observations—though even here our choice is broadening, and can be broadened much more with the use of modern information storage and retrieval equipment.

Perhaps because we have had to choose we have, at various times, favored certain kinds of observations and ignored others. In classifying both our kinds of data and our kinds of individuals, we have favored successively the medicinal qualities of plants, their floral morphology, their "genetically determined" characters, and most recently, those characteristics that are thought to be most important in revealing their phylogenetic histories. Other criteria some of us have chosen, with

sometimes the near exclusion of all others, have been plant chemistry, ecological relationships, and cytology.

Many, though not all, of us believe more and more today that taxonomy has a function more important than yielding to the philosophy or the hypothesis of each age —that the classification of animals and plants should be, if possible, independent of these hypotheses but nevertheless more useful to them than it is now. Theories of the workings of the universe change; this we should certainly know by this time, if we have any knowledge of history. There is very probably no absolute reality—or, in any event, we have no way of knowing whether we have yet found it, and every philosophical reason to believe that we have not. This has been most forcibly presented to us by modern philosophers and physicists, such as Bridgman, Woodger, Reichman, Schrödinger, and Einstein.

Two theories, by which we set much store and which we have used to repattern our taxonomies, are the gene theory and the theory of evolution by natural selection. Perhaps we may ask a question of each that will reveal their nature. The gene theory is based primarily upon the recognition or acceptance of a hypothetical elusive atom called the gene, said to be located at a specific place on a chromosome and to have one or more specific hereditary effects. But we find ourselves in the position of the physicist looking first for the atom and then the electron. When our instruments or techniques become elaborate enough to find our electrons and genes they are no longer there—and we cannot even surely locate a single point of origin for the phenotypic effect we can observe. What then is the "gene?" It is, of course, a temporary working model which may always be useful but can no longer be accepted as a real thing existing, we may say, outside the minds of men.

To doubt that Darwinian evolution theory is the final, perfect explanation of the organic universe is sheer heresy today, but I do not see how we can but doubt it. Certainly there may be much truth or usefulness in the theory, but as certainly there is much that will be discarded when it is someday replaced by broader, more inclusive, and more useful theories. How is it possible to accept it so completely when there have been so few quantitative or logical tests of it—when, as a matter of fact, we have been unable as yet to devise an adequate test of it, being limited to such a brief sample of the universe. Our evidences are nearly all indirect—inferences from "similarities" and "differences" which themselves are the result of arbitrary classifications. It does have wonderful emotional appeal though, for, like the theory of special creation, man still finds himself at the top of every evolutionary chart. I would like to ask what *scientific* value a theory has that ends this way? Though I do believe that Darwin had begun to understand man's significance or his insignificance at times, we have added the emotional features, the old neurotic drives, from our previous theologies, and in most of our evolutionary studies are primarily playing games again, fitting the universe to our capricious, wish-fulfillment drives, rather than observing it as it may be.

I would like to suggest a taxonomic approach to the universe which I believe is not only more objective than our present approach but will eventually be far more useful to us and particularly to future taxonomists. It rejects genetic and evolution theory as bases for a general taxonomy. For this reason, it may be more useful for, as I have said, we cannot expect these theories to be "true"—or to continue forever as useful to us in scientific research as they are now.

In physical research a revolution in method of approach, initiated by Galileo and spurred by the so-called "phenomenalists," has occurred in the past few decades, and it has proven tremendously fruitful. The theoretical physicist has had to become, of necessity, a philosopher,

an occupation of great distaste to most scientists. This can be understood because the experience of most of us in philosophy has been with the unreal emotional approaches of such philosophers as Kant, Spinoza, and Nietzsche. Philosophy has become something quite different today, much more objective and more closely allied with our own scientific efforts.

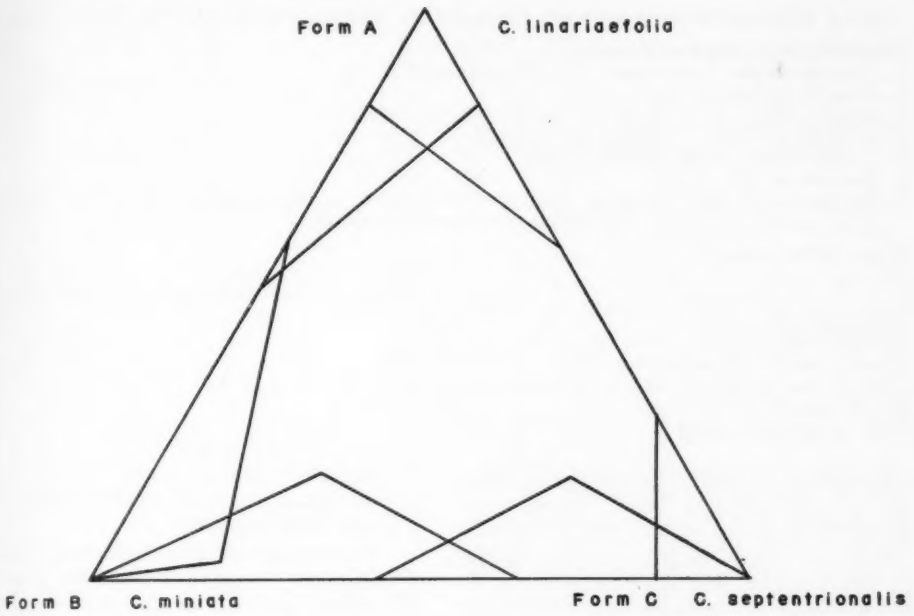
The operational approach to physics, as defined by Bridgman (1936), was explained by him in the following quotations: ". . . for me meaning is to be found in a recognition of the activities involved." ". . . Einstein recognized that in dealing with physical situations the operations which give meaning to our physical concepts should properly be physical operations, actually carried out. For in so restricting the permissible operations, our theories reduce in the last analysis to descriptions of operations actually carried out in actual situations, and so cannot involve us in inconsistency or contradiction, since these do not occur in actual physical situations." "The operational point of view would say that the relation comes into existence when it is discovered." ". . . the dictum of the operationist that only those physical concepts have meaning that can be defined in terms of physical operations, which means in particular that no quantitative physical concept has meaning unless it corresponds to something measurable."

How may this approach be applied in biology? I believe that we must first make an effort to distinguish between the operations we perform and the conclusions or hypotheses we draw from them. Next we need to concentrate on refining our operations and ordering and storing adequately the data we derive from them. We will of course wish to interpret our data, to construct various hypotheses, as this is presently a human desire and need.

I would like to present portions of two studies, both incomplete, to illustrate a somewhat different and, I believe, more objective approach to the description of organisms. The first concerns the genus *Castilleja* (Scrophulariaceae), a taxonomically difficult group of North American wildflowers, commonly called the Indian Paintbrushes. There is no agreement among taxonomists about the number of species, or the taxonomic meaning of the considerable morphological and ecological variation that is apparent in the many forms. With the assistance of students[1] at the Rocky Mountain Biological Laboratory, Gothic, Colorado, a local study was made during the summer of 1960. Samples of specimens were obtained at three elevation ranges in the Gothic area in Gunnison County, Colorado. Results of the study in the 9,000′ to 10,000′ elevation range will be discussed here.

No initial attempt was made to identify the forms in the Gothic area by means of taxonomic keys or descriptions. Visually there appeared to be three fairly distinct morphological and ecological forms, and four samples of 25 plants each were taken of each form. These specimens were then carefully examined, and those characteristics differing most markedly among the three more-or-less subjectively chosen forms were measured or scored. Following this, three inter-sample comparisons were made, between each pair of forms. These comparisons were made by indexing the measurements (as shown later in the paper in the discussion of *Viola adunca*), with low values being assigned to properties characteristic of one form and high values to properties characteristic of the other. Each specimen was then scored, and the distributions of scores plotted on graph paper. The final results of these inter-form comparisons are shown in Figure 1. Each corner of the triangle represents one of the forms, the name assigned representing that to which it most easily keyed in Harrington (1954). The curves have been simplified to show only the range of total variation for each

[1] Eleanor Ryan, University of Washington, and Michael Mertens, University of California at Riverside.



form, based upon a comparison with another form, and the position of the mode.

The significance of this graph is that it presents a visual picture of each form, *as it exists with respect to two others.* I believe that our knowledge or definition of things in nature is derived entirely from comparison, and that in the present instance a beginning has been made towards the numerical definition of certain forms of *Castilleja,* in relation to other morphologically similar forms. Many more comparisons will be necessary for each form recognized before its definition approaches any degree of completeness. And, of course, the comparisons must be extended to include more than morphological differences. In no case can we expect to complete the definition of an object, organic or inorganic, as this would require comparisons with every other object in the universe, in every property in which they differ. This seems a hopeless task for even any type of computer we might build in the future and certainly is for present models. But in any event we should be able to obtain more precise definitions or descriptions of objects following techniques of this sort than we have been able to achieve in the past.

The second study [2] concerned a kind of violet (*Viola:* Violaceae), the taxonomic status of which has also been a matter of controversy. It has been called *Viola adunca* J. E. Smith; at higher elevations a form similar to this has been recognized by some taxonomists and called *Viola bellidifolia* Greene. After a careful examination of plants from various locations in Colorado a number of morphological characteristics were chosen for measurement or scoring. Only those which showed considerable inter-individual differences were chosen, and the seven eventually used in the analyses are listed in Table 1. Sixteen mass collections were made from the 16 areas in which the violets were seen during the summer of 1960, and measurements were made on each of the 25 plants of each sample. After the ranges of meas-

[2] Measurements of the specimens were made by Stephen Koch, Swarthmore College.

TABLE 1—CHARACTERISTICS USED AND INDEX VALUES ASSIGNED FOR SAMPLES OF *Viola adunca*.

Characteristics measured or scored:

1. Length (in mm.) of a large, mature leaf blade.
2. Breadth of this lamina.
3. Distance from the apex of this lamina to a basal lobe.
4. Number of teeth on one-half this lamina.
5. Length (mm.) of the largest stipule.
6. Breadth of this stipule.
7. Pubescence on four leaf areas: upper surface, lower surface, margin, and petiole. Scored on a quantitative scale: 0–glabrous to 8–heavily pubescent.

Index values assigned:

CHARACTER	VALUE 0 (BELLIDIFOLIA)	VALUE 1 (INTERMEDIATE)	VALUE 2 (ADUNCA)
Lamina length (mm.)	6–20	21–30	31–55
Lamina length/breadth ratio	1.21–1.50	—	0.81–1.20
Lamina length/length to lobe ratio	1.01–1.35	—	0.86–1.00
Teeth ½ lamina/lamina length ratio	0.80–1.19	0.50–0.79	0.10–0.49
Stipule length/breadth ratio	1–6	—	7–18
Total pubescence value	0, 1	2–6	7, 8

urements were plotted for the characteristics of each sample, index values were assigned as discussed for *Castilleja* above (Table 1). Next, each plant was scored in each sample, and the distributions of index scores for the collections are shown in Table 2. From these distributions we may observe that, with a few exceptions, the higher elevation collections (*"bellidifolia"*) had low scores, and the low elevation samples (*"adunca"*) had higher scores.

On the basis of this chart (Table 2), a taxonomic decision might be made regarding the disposition of *"bellidifolia"*, but without further analysis some artificial criterion would have to be chosen. These data were further analysed or described as follows.

Each of the 16 index distribution curves was compared with each of the other 15 index distribution curves using the following four criteria:

1. Percentage of the total range of index variation common to the two samples which the sample in question did not cover.
2. Percentage of the total range of the distance or part between the two modes of the distributions being compared.
3. Percentage of the distance of the total range from the mode of the sample being compared to the end of the range most characteristic of the other sample.
4. Percentage of the total range not covered by either sample (plus value) or of that portion of the range covered by both samples (minus value).

The aim of these four measurements was to illustrate the total amount of difference between the two aggregations being compared. Statistical techniques might also be used to compare these, but in my opinion ordinary statistical techniques are less than perfect for describing organic variation, principally because they demand comparisons with nonexistent, idealized variation curves, the results being therefore not descriptions of actual variation but hypothetical constructs farther removed from the organisms than necessary. This was recognized by Clausen (1960) who said: "Statistical methods are at best only crude tools for the determination of phenotypic variability. The variation curve is a better biometrical description of the variability of a character within a population than are statistical means, variance, and standard deviations that tend to submerge the pattern of the variability."

In each of the above cases, a double comparison was necessary. *Each* sample

TABLE 2—DISTRIBUTIONS OF DIFFERENCE INDICES (PERCENTAGES) FOR SAMPLES OF *Viola adunca*.

TABLE 2—DISTRIBUTIONS OF DIFFERENCE INDICES (PERCENTAGES) FOR SAMPLES OF *Viola adunca*.

Index Number	Sample Number (% of specimens) 60–34	60–141	60–83	60–35	60–31	60–142	60–139	60–29	60–138	60–140	60–32	60–28	60–27	60–30	60–22	60–61
12																12
11													4	4	16	32
10												16	16	22	24	20
9									4			8	16	30	28	20
8								4		4	8	40	20	13	16	12
7		4					4	8	4	4	10	24	28	22	4	
6	8			8	8		4		16	12	10		16	9	4	
5		4	8	12	12	8	12	16	4	16	33	12				4
4	23	16	12	20	12	20	36	32	20	20	21					
3	8	24	40	8	36	40	12	4	20	20	6					
2	31	12	16	24	16	12	12	16	24	4	10					
1	15	36	20	4	16	20	8	20	4	16	4					
0	15	4	4	24			12		4	4						
No. of spec.	26	25	25	25	25	25	25	25	25	25	48	25	25	23	25	25
Mean Index	2.38	2.44	2.60	2.64	2.76	2.84	3.24	3.60	3.72	3.76	4.96	7.80	8.00	8.17	8.36	9.92
Elev.	11400	11600	11400	10800	10000	11600	11000	11500	11000	11000	10300	10100	10100	8400	8400	9000

had to be compared with *each* of the others, as the object was not to describe non-existent "relations" between them but the samples themselves as they existed (in terms only of the measurements or operations made) with reference to the other samples.

When the four curve or index distribution comparative percentages were added they yielded a single figure ("difference index") which, under the terms defined above, can be considered to represent total difference. The matrix obtained is shown in Table 3, and represents the results of all the possible comparisons. From this, as from Table 2, we see two fairly distinct sets of samples or collections.

At this point the descriptive analysis, from the measurements collected in this study, is complete. The next question of concern to the taxonomist is how to use this analysis for purposes of classification, and I consider this without the scope of the present paper. I believe that until we have a moderately large number of such analyses, it will be foolish to attempt classification. Some of the difficulties we encounter with our present Linnaean scheme are due to the fact that it was set up with far too small a sample of both the properties of organisms and numbers of them. The type of analysis presented here will begin to show us the actual kinds of *relative* variability present in nature and will illustrate them in a numerical language, one that will lend itself much better to logical and mathematical techniques of classification, such as Dr. Mason presented in the previous paper. Such analyses as these may eliminate the vexing and unrewarding searches for "species," "genera," "families" and other categories in nature by actually illustrating the presence or absence of aggregations of various magnitudes "in nature." I believe that they will also help eliminate the "search for order" in nature. Nature has its own order or disorder; there is no reason to suppose that it corresponds to any of the sorts of "order" (theological, genetic,

TABLE 3—MATRIX OBTAINED BY COMPUTING DIFFERENCE INDICES AMONG 16 SAMPLES OF *Viola adunca*.

	60–61	60–28	60–22	60–30	60–27	60–34	60–29	60–140	60–139	60–138	60–31	60–142	60–83	60–32	60–141	60–35
60–61	x	75	72	128	128	153	157	165	165	173	175	179	181	187	188	192
60–28	50	x	38	49	35	164	130	141	140	150	150	155	158	120	168	173
60–22	27	38	x	25	50	153	122	133	133	141	141	146	150	109	158	162
60–30	85	35	12	x	33	179	149	154	134	200	168	175	175	140	184	188
60–27	113	21	62	50	x	146	113	124	125	133	131	136	141	104	150	154
60–34	184	174	145	171	155	x	77	67	57	65	28	35	28	77	45	39
60–29	141	100	113	122	104	43	x	12	5	30	13	18	44	13	49	54
60–140	138	100	113	109	104	17	12	x	12	5	11	18	11	23	23	28
60–139	142	104	116	100	108	31	5	6	x	20	25	31	25	22	38	44
60–138	150	114	125	133	117	—15	50	40	50	x	50	60	50	60	—10	—5
60–31	184	150	159	168	149	28	63	50	38	20	x	84	14	—10	38	43
60–142	196	165	174	185	164	35	81	68	56	25	41	x	25	97	42	50
60–83	181	149	142	167	150	14	72	61	50	10	14	—9	x	72	25	29
60–32	148	80	91	104	86	55	13	40	34	50	24	59	50	x	72	77
60–141	188	159	158	174	158	—18	83	73	55	50	62	66	62	94	x	—31
60–35	200	173	170	188	174	—24	99	89	82	85	57	64	57	110	44	x

phylogenetic, etc.) that we attempt to impose upon it.

My hope in this talk is not to convince you that the particular method of description by comparison that I have shown has any unusual value, but that some real attempt must be made by taxonomists to achieve a greater amount of objectivity (recognition and analysis of sense impressions) in their approach. Biology, to a greater degree than most other sciences, tends to put the investigator on a throne (or under the feet of someone on a throne). It is dominated by tradition and has a set of almost inflexible rules. We *must* "believe in" certain concepts and follow certain procedures. And yet the progress of human knowledge comes from genuine, perpetual doubt and the willingness and desire to attempt new ways of thought, new organizations and evaluations of our data. To progress, we must know that at any time our interpretations of the universe are wrong. Further, we must realize the profoundness of our ignorance of the universe; the sample of it that we have carefully observed is minute. May I end with two quotations:

"Human knowledge concerning the material universe is never complete, nor is it to be regarded as ultimate truth, but rather as provisional, fragmentary, subject to extension, to revision and to reformulation in the light of future observation, experiments, and correlative investigations." (Perry, 1960)

"No one can fairly deny that at present there are two effects of the Darwinian mode of thinking. On the one hand, they are making many sincere and vital efforts to revise our traditional philosophic conceptions in accordance with its demands. On the other hand, there is as definitely a recrudescence of absolutistic philosophies; an assertion of a type of philosophic knowing distinct from that of the sciences, one which opens to us another kind of reality from that to which the sciences give access; an appeal through experience to something that essentially goes beyond experience. This reaction affects popular creeds and religious movements as well as technical philosophies. . . .

"Old ideas give way slowly; for they are

more than abstract logical forms and categories. They are habits, predispositions, deeply engrained attitudes of aversion and preference. Moreover, the conviction persists—though history shows it to be a hallucination—that all the questions that the human mind has asked are questions that can be answered in terms of the alternatives that the questions themselves present. But in fact intellectual progress usually occurs through sheer abandonment of questions together with both of the alternatives they assume—an abandonment that results from their decreasing vitality and a change of urgent interest. We do not solve them: we get over them. Old questions are solved by disappearing, evaporating, while new questions corresponding to the changed attitude of endeavor and preference take their place . . ." (Dewey, reprint 1957)

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Has the Biological Species Concept Outlived Its Usefulness?

PAUL R. EHRLICH

IN THE PRESENT PAPER I would like to consider the following question: Is the biological species concept a useful taxonomic tool? I do not wish to reexamine the philosophical question of whether or not there really are distinct entities in nature which correspond to our idea of "biological species." This problem has been dealt with fully by Burma (1954), Mayr (1957a), and others. In addition I will ignore the related question of the degree to which apparent structuring in nature is an artifact caused by the structuring of the vertebrate central nervous system or by the thought patterns characteristic of Western culture.

Whatever its degree of reality, there is no doubt that in the past the biological species concept has been useful in helping to shape our thinking about evolutionary problems. No one familiar with the "modern synthesis" in evolution would deny that reproductive isolation is a major factor in the evolutionary process. It does, however, seem pertinent to question (even at the risk of being accused of embracing the heresies of typology and anti-evolutionism) using this isolation as a criterion for a taxonomic grouping. Grant (1957:74–75) states

"According to the biological species concept the species is a population set apart from the rest of the living world by reproductive isolating mechanisms. Its boundaries therefore should be marked by a prominent gap in the variation pattern. Good discrete species are in fact found in all major plant groups. These well-defined species, however, constitute only a fraction of the populations in their respective phylads. The botanist finds problematical species intermixed in varying proportions with good species in most of the families and genera. This is in marked contrast with the situation which the zoologist finds in higher

animals in which clearly circumscribed species are a rule and poorly defined ones the exception."

In a sample survey of some genera of plants, Grant found the percentage of "good" (i.e., distinct or easily delimited) species to range from 0 (California *Ceanothus*) to 100 (North American *Asclepias*).

There seems to be general agreement that the biological species concept has no meaning whatever when one is dealing with asexual organisms, and is quite limited in its applicability in plants. However, what of the higher animals where "circumscribed species are the rule and poorly defined ones are the exception?" Mayr (1957b) has suggested that analyses such as were done by Grant should be carried out for as many groups of plants and animals as possible. As a preliminary step in considering the usefulness of the concept, I have done such a survey of a group with which I am familiar, the Nearctic butterflies (Papilionoidea).

There are few, if any, groups of equivalent size that are as well-known systematically as the butterflies. Vast collections of them have been amassed, and the literature is replete with observations on their distribution and (to a lesser degree) their genetics and behavior. If the biological species concept is useable, it should be easily applicable to a well-known, diploid and outcrossing group of "higher" animals such as the Nearctic butterflies.

In my survey of the butterflies, several things were done which would tend to overemphasize the utility of the biological species concept. First of all I was surveying a limited fauna, and it is widely admitted that species are more clearcut when viewed within a limited geographical area. Thus the problem of the specific distinctness (or lack of same) of the Nearctic representatives of Holarctic forms was not considered. In addition the question of possible undetected reproductive barriers was ignored. In other words, forms having a wide spatial distribution, but superficially not showing great geographic variation, were not considered as presenting any problem at the species level—although interfertility may *not* always exist where it is assumed.

The genera of North American butterflies are grouped below (somewhat arbitrarily) into seven categories, according to the frequency of "good" species found within them. It was rather difficult, in many cases, to decide exactly which category was proper for a given genus, which in itself would cast doubt on the overall utility of the species concept. If biological species were readily recognizable, we would have no difficulty in classifying genera according to the proportion of distinct species found within them.

Group 1. Genera in which the species seem quite distinct, and are considered by most workers to present no serious problems: *Parnassius, Neophasia, Phoebis, Lethe, Euptoieta, Poladryas, Microtia, Nymphalis, Vanessa, Anartia, Calycopis, Erora, Brephidium, Apodemia.*

Group 2. Genera in which most species seem distinct, but the status of some forms is in doubt at the present time: *Eurema, Anthocaris, Euchloe, Euptychia, Erebia, Ministrymon, Euristrymon, Strymon, Philotes.*

Group 3. Genera in which many or most forms present serious problems: *Papilio, Pieris, Oeneis, Speyeria, Boloria, Euphydryas, Chlosyne, Phyciodes, Polygonia, Precis, Limenitis, Anaea, Libythea, Chlorostrymon, Satyrium, "Thecla," Callophrys, Lycaena, Plebejus, Everes.*

Group 4. Genera in which, at the present state of our knowledge, the biological species concept is virtually inapplicable: *Colias, Coenonympha, Cercyonis.*

Group 5. Genera which are monobasic: *Paramecera, Neominois, Agraulis, Dryas, Dryadula, Habrodais, Hypaurotis, Phaeostrymon, Chrysophanus, Dolymorpha, Hypostrymon, Panthiades, Glaucopsyche, Phaedrotes, Celastrina.*

Group 6. Genera which are not well represented in the Nearctic region, but

best information would indicate that they belong in Group 1 or Group 2: *Nathalis, Anteos, Historis, Eumaeus, Leptotes.*

Group 7: Genera which are not well represented in the Nearctic region, but best information would indicate that they belong in Group 3 or Group 4: *Battus, Graphium, Parides, Enantia, Lycorella, Heliconius, Metamorpha, Hypolimnas, Myscelia, Diaethria, Eunica, Mestra, Hamadryas, Biblis, Dynamine, Marpesia, Apatura, Tmolus, Cyanophrys, Atlides, Electrostrymon, Hemiargus, Agriades, Zizula, Euselasia, Emesis, Lasaia, Caria.*

Some of the genera listed under Group 7 may well move into Group 6 when we know more about the many tropical groups represented there. I will confine my further comments to those genera in the first four groups.

I would like to discuss a few of the genera in greater detail in order to give some idea of the necessarily rather loose standards employed in assigning them to the different categories.

Nymphalis will serve as an example of the genera with distinct species (Group 1). The recognition of four distinct segregates (*antiopa*,[1] *milberti, californica,* and *vau-album*) in North America dates at least back to Morris (1862), and to my knowledge this arrangement has never been seriously challenged. Specimens may be assigned to one of the four forms with certainty. It should be noted, however, that only the "rules" listed earlier prevent our removal of the genus from this category. There is considerable doubt as to the relationship between the Palaearctic and Nearctic forms recently lumped as *vau-album.* For many years the Nearctic form was considered specifically distinct and went under the name *j-album.*

Erebia is a genus typical of those in which most species seem distinct (Group 2). Ignoring the status problem of our members of Holarctic series, and the possible reproductive incompatibility of individuals from various populations of widely and discontinuously distributed "species" such as *theano,* we find eight distinct segregates (*theano, discoidalis, vidleri, callias, disa, rossii, youngi,* and *epipsodea*), and one difficult complex (*magdalena-mackinleyensis-fasciata-avinoffi*). It seems unlikely that this complex will ever prove amenable to pigeonholing.

Papilio is a large genus containing many taxonomically refractory complexes (Group 3). Most outstanding in North America is the *machaon* complex. A quote from Remington (who has been working on the elucidation of the genetic relationships of forms in this complex) will serve as an illustration of the difficulties encountered. He discusses (1958) the forms of the *machaon* complex in the Riding Mountain region of Manitoba and tentatively concludes:

> "1) Riding Mountain is the locus of origin of *P. kahli,* an isolated, distinctive offshoot of *P. polyxenes* with black wings, spotted abdomen, and large acentric "pupil." 2) In relatively recent times *P. machaon* arrived on the plateau, perhaps carried from Alberta in hay or straw during the development of the National Park or of highways or railroads. 3) These two *Papilio* at first lacking behavioral and other isolating mechanisms, hybridized rather freely; the distinctive genotype of *P. kahli* allows the F_1 heterozygotes to show some yellow-wing characters never seen in laboratory crosses of *machaon* with true *polyxenes.* 4) Since *P. kahli* and *P. avinoffi* belong to separate species, one expects that isolating mechanisms are evolving in Riding Mountain populations and that eventually natural hybrids will no longer be produced. Meanwhile, each species may be incorporating into its genotype new adaptive alleles from other species (introgression). There is little basis

[1] The continued presence of authors' names following the names of species of North American butterflies is, in most cases, a waste of type. Starting with this paper I will only cite author's names where there is some conceivable chance of confusion. It is strongly urged that the trivial names in the forthcoming dos Passos checklist be adopted by all persons interested in Nearctic butterflies, and that no changes be made in them except where retention of a name might lead to confusion. Citation of authors' names as a matter of course should cease.

for regarding *kahli* as dimorphic, in the sense of *P. glaucus* females. For the present, these Riding Mountain swallowtails may be called *P. kahli* (or *P. polyxenes kahli*), *P. machaon avinoffi*, and their hybrids."

There is no reason to believe that similar situations do not exist throughout the complex.

Pieris is included in this category because of the complete confusion regarding the status of the *protodice-occidentalis-calyce-sisymbrii-beckerii* series of forms. *Oeneis* is placed here because, among other problems, the scope of the "species" *chryxus* is a matter of differing taste, and this series of forms cannot be separated with assurance from British Columbian forms usually lumped in with *taygete*. The White Mountain butterfly, *Oeneis semidea* and its Rocky Mountain relative *O. lucilla* are, at present, considered part of the "species" *melissa*, although there is no genetic evidence to support this placement. Similarly only a look at the latest butterfly book will tell one whether or not the Mt. Katahdin butterfly, *O. katahdin* and its Cordilleran relative *O. brucei* are in or out of the species *polixenes*. In *Speyeria* an array of 109 names was reduced by dos Passos and Grey (1947) to a group of 13 "species." However, no evidence has ever been presented which would indicate that there are actually 13 biological species in *Speyeria*—although there seems to be general agreement that most or all of the 13 segregates represent related series of clusters.

The three genera in the "concept inapplicable" category (Group 4), all have the same thing in common. That is that no two people seem to be able to agree on what are or are not "species" among the observed segregates within these genera. Consider, for example, the genus *Coenonympha*. One very distinct form, *haydenii*, is universally considered to have specific status. However, the remaining array of Nearctic forms have been considered to be conspecific (e.g., Davenport, 1941), to be a series of species and subspecies within a superspecies (Brown, 1955), or to be a series of full-fledged species (most earlier authors). At the moment we have no real evidence on the genetic relationships of any of these forms, and thus no way (except guesswork) of coming to a decision as long as we insist on employing genetic standards.

What can we conclude from this crude survey of the Nearctic butterfly genera? Above all else we can say that, *at least at the present level of knowledge*, the prevalence of the clearly defined species is a myth. Even biasing the survey in favor of the distinctness of species, about one-half of the genera resist partitioning.

This result is really not surprising, as the very nature of the biological species definition makes its use impossible in practice. The only test of conspecificity (or lack of same) is what happens when two forms occur together *in nature*, and, even when sympatric organisms can be studied, partial interbreeding may make a clear decision impossible. Genetic tests in the laboratory, while yielding valuable information, are never definitive. Organisms which are sympatric but remain distinct in nature may freely interbreed in the laboratory. Conversely, organisms placed together in the laboratory may be unable to interbreed successfully, although populations of the same organisms approaching each other gradually in nature may be quite capable of blending together. Mayr (1957b: 378) points out that this indeed might be the case with the laboratory-isolated northern and southern *Rana pipiens*. Of course, one could define the biological species in such a way that laboratory tests would be conclusive, but even if this were done the amount of work involved in clearly delimiting a single species would be staggering. It seems clear that the biological species is not a practical taxonomic category.

It might be noted parenthetically that casual discussions with other zoological systematists (an ichthyologist, a herpetologist, and a hemipterist among others)

lead me to believe that the abundance of clearly delimited segregates in the higher animals has been vastly overestimated. The situation in mammals may well be inferred from the following quote from Hall and Kelson (1959, volume 1, page v):

> "The taxonomic limits assigned to any order or genus or intermediate taxonomic category reflect our own personal judgment. For specific versus subspecific status of any kind of mammal, we have accepted the last-published *opinion* that *was supported by evidence obtained from examination of specimens.*" (my italics)

There seems to be no reason why taxonomy at the "species" level should not be approached in the same way as is the taxonomy of higher categories. Quantitative studies of phenetic relationships will reveal clusters of populations, and where it is convenient for purposes of communication we can give formal names to these clusters. *The genetic relationships of the clusters* (i.e., *the degree of interbreeding among them*), *when known, will be important attributes of the clusters, but will not be involved in category definition.* Using such a system it seems obvious that any organisms sufficiently distinct to be sympatric without interbreeding will fall in distinct clusters, although as in classical taxonomy, polymorphism will cause a certain amount of difficulty.

It should be emphasized that the removal of degree of isolation as a criterion for "membership" in a systematic category *in no way lessens the evolutionary importance of such isolation.* It is merely recognition of the difficulties of defining the necessary level of isolation, and then of determining whether or not that isolation exists.

There probably is a point in the hierarchy below which grouping organisms on the basis of their overall similarity (rather than imagined phyletic relationships) will result in similar individuals from different Mendelian populations being grouped together, rather than individuals from the same population. Since Mendelian populations have properties not possessed by their component individuals, such groupings of similar individuals from different populations could be considered "unnatural." This does not mean, however, that such groupings are devoid of biological interest. In order to test the hypothesis that numerical analysis will not cluster individuals by population, a pilot study was undertaken in which the similarities of an array of individual butterflies were evaluated. Thirteen male specimens of the genus *Euphydryas* were selected for study—10 from four populations identified as belonging to the species *E. editha,* and three from the closely related species *E. chalcedona.* In at least some areas (e.g., the vicinity of San Francisco) populations of *editha* and *chalcedona* coexist without signs of hybridization. The specimens, all selected at random from longer series, came from the following localities:

3 *E. editha* (SB600, SB601, SB602): San Bruno Hills, San Mateo County, California, elevation 600 feet, April 3, 1960.

3 *E. chalcedona* (CHAL565, CHAL566, CHAL567): Pinnacles National Monument, San Benito County, California, elevation 1300 feet, April 26, 1959.

2 *E. editha* (KING8461, KING579): Kings Canyon National Park, California, elevation 9–10,000 feet, July 20–21, 1958.

3 *E. editha* (WOOD611, WOOD612, WOOD613): Woodside Experimental Population, San Mateo County, California, elevation 540 feet, March 22, 1961.

2 *E. editha* (MONT6008, MONT6010): Route 198, 20 road miles east of Route 101, Monterey County, California, elevation 2500 feet, April 20, 1960.

Because of the ready availability of a Burroughs 220 Algol program for computing product-moment correlation coefficients I decided to do classical correlation

and weighted variable group (WVG) analyses of the phenetic relationships of the 13 individuals. This procedure is thoroughly outlined in Sokal and Michener (1958) and will not be discussed further here. Table 1 lists the 74 characters used in the study, and the number of states into which they were divided. Because of the

TABLE 1—CHARACTERS EMPLOYED, WITH NUMBER OF STATES INTO WHICH EACH WAS DIVIDED SHOWN IN RIGHT HAND COLUMN. V = VENTRAL, D = DORSAL, FW = FOREWING, HW = HINDWING.

1.	Width of large cream spot in FW discal cell	7
2.	Shape of large cream spot in FW discal cell (ratio)	6
3.	Width of orange spot in FW discal cell	9
4.	Position of proximal cream spot in FW cell M_3	6
5.	Color of proximal spot in FW cell Cu_1	4
6.	Width of cream spot in FW cell Cu_1	6
7.	Width of distal red spot in FW cell M_3	4
8.	Width of proximal cream spot in HW cell M_2	4
9.	Shape of proximal cream spot in HW cell M_2 (ratio)	5
10.	Amount of orange in proximal cream spot in HW cell M_2	4
11.	Width of cream half-moon spot in HW discal cell	4
12.	Percentage of light scales in proximal orange spot in HW cell M_2	4
13.	Separation of proximal orange and white spots in HW cell Cu_1	4
14.	Width of proximal orange spot in HW cell M_3	4
15.	Width of distal cream spot in HW cell M_3	4
16.	Length of forewing	5
17.	Shape of forewing (ratio)	6
18.	Comparison of VFW and VHW patterns	3
19.	Palpus color	3
20.	Color of abdominal dorsum	3
21.	Color of abdominal venter	3
22.	Degree of fusion of half-moon spot in HW discal cell with basal spot	3
23.	Shape of distal cream spot in HW cell M_3	3
24.	Color of DHW anal margin	3
25.	Condition of orange marginal spots of DHW	3
26.	Condition of dark line in white median band of DHW	3
27.	Color pattern of antennae	2
28.	Shape of abdominal sternum 6	2
29.	Shape of abdominal tergum 2	2
30.	Shape of tegula	3
31.	Form of joining of mesopreepisternum and mesokatepisternum	3
32.	Form of dorsal part of pleural suture	2
33.	Shape of anterior part of spinasternum	2
34.	Length of middle segment of palpus	6
35.	Width of face at tentorial pits	6
36.	Width of frontoclypeal sclerite between antennae	4
37.	Ratio of spread of pilifers to face width	5
38.	Shape of vertex of head	2
39.	Height of metaepimeron	4
40.	Length of uncus lobes	2
41.	Condition of tegumen just anterior to uncus lobes	3
42.	Form of saccus lobes	3
43.	Position of tips of valvae	3
44.	Shape of juxta	2
45.	Shape of process of juxta	2
46.	Depth of cleft between teeth of ventral arm of clasp	2
47.	Height of inner face of lip of valva	2
48.	Form of dorsal arm of clasp	3
49.	Length of aedeagus	7
50.	Height of valva	7
51.	Shape of aedeagus (ratio)	6
52.–64.	Characters of forewing venation	

TABLE 1—*Continued*

52. Distance between tips of R_4 and R_5 5
53. Distance between tips of R_5 and M_1 6
54. Distance between tips of M_1 and M_2 6
55. Distance between tips of M_3 and Cu_1 5
56. Distance between tips of Cu_1 and Cu_2 5
57. Distance between tips of Cu_2 and 2V 4
58. Distance from R_4-R_5 crotch to tip of Cu_1 4
59. Length of mdc 5
60. Length of ldc 6
61. Length of M_3-Cu_1 stalk 8
62. Length of M_3-ldc stalk 6
63. Length of free M_3 5
64. Length of free R_4 5
65.–74. Characters of hindwing venation
65. Distance between tips of M_1 and M_2 5
66. Distance between tips of M_2 and M_3 4
67. Distance between tips of M_3 and Cu_1 5
68. Distance between tips of R_5 and Cu_1 5
69. Distance between M_1-R_5 crotch and Cu_1-Cu_2 crotch 4
70. Length of udc 5
71. Length of free M_2 4
72. Length of free M_3 5
73. Length of M_3-Cu_1 stalk 4
74. Distance between Cu_1-Cu_2 crotch and tip of 2V 6

ease of computation [2] it was possible to calculate the Q-matrices (specimen x specimen) for the following combinations of characters: 1–74; 1–16; 1–27; 28–51; 52–74; 1–27 and 40–74; 1–27 and 40–51; 1–27 and 52–74; odd numbered characters; and even numbered characters.

The R-matrix (character x character) was also obtained for all characters based on the coded data. However, because the coding forces us to evaluate each of the 2701 coefficients separately, and because of the low number of observations per character (13), a second R-matrix was computed for the first 16 characters using uncoded data and 9 additional specimens from the same populations. Because of the large number of measurements used as characters, these matrices as well as the raw data were carefully examined for evidence of repeated insertion of a general size character (especially in view of the slightly larger average size of the three *chalcedona* specimens). There was no sign of a significant weighting of size—in the R-matrices, the original data, or the way the specimens clustered.

The Q-matrix based on all 74 characters is shown in Table 2 (coefficients greater than .25 are significant [$P < .01$]).

A number of interesting points emerge in examining the Q-matrices. In eight of the nine Q-matrices (including 1–74) the three *chalcedona* specimens had higher correlations among themselves than any one of them had with a non-*chalcedona* specimen. Interestingly, the only matrix where this was not true (28–51) was the one containing the structural characters (genitalic) normally considered "important" or "basic" by the old line taxonomists. However, as was expected, with the exception of the two Kings Canyon specimens, there was little tendency for the various *editha* to assort according to their population of origin. The results of the WVG search for structure in the matrix are shown in Figure 1. The Kings

[2] The actual preparing and measuring of the specimens took several days. The computation of 3601 correlation coefficients (plus means and standard deviations of the variables) took 20 minutes. Including punching of the data onto cards the total computational cost was about $25.00. The same computations on a desk calculator would take a competent operator about two years of full-time work.

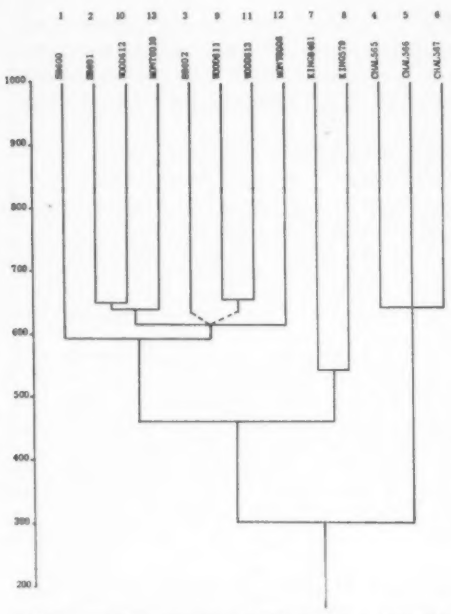

FIG. 1. Diagram of relationships obtained by the weighted variable group method ($L_n = .045$). Ordinate is the correlation coefficient multiplied by one thousand.

Canyon specimens had been determined by the collector as *editha* (on the basis of facies and presumed food plant), but in the most recent key (Bauer, 1961) they run to *chalcedona* on the basis of genital structure. The diagram of relationships clearly shows their position as a distinct group of the *editha* cluster. It can also be seen by examination of the original matrix that, among the *editha* specimens, KING579 has the highest average correlation (.374) with the three *chalcedona*, and that KING8461 has the third highest (.249). This information is lost in the process of determining structure. The genus *Euphydryas* has long resisted satisfactory treatment by classical methods—a thorough numerical study would doubtless go a long way towards the description of the relationships of the various clusters of populations.

A number of tentative conclusions may be drawn from this pilot study. First, the numerical method, even using relatively unrefined techniques, seems to be quite able to associate what are considered on other grounds to be related entities. Indeed, it can do this with characters (e.g., 52–74) which, to my knowledge, have never been utilized in classical taxonomic studies. Furthermore, the information content of the matrix, as well as that of the derived structure, is vastly greater than that usually supplied in a standard taxonomic work. On the basis of this information one might wish to hypothesize that the Kings Canyon population split off from the other *editha* after an *editha-chalcedona* split, or that *chalcedona* represents a rapidly evolving line originating from a Kings Canyon type stock. A firm base is provided for speculation, *but the speculation is not involved in establishing the base.*

The failure of the technique to assort individuals into groups corresponding to their population of origin is not disturbing. There is nothing to be gained in extending the taxonomic system to this level, since the process of gathering the samples *automatically assorts individuals into geographic clusters.* However, it might be very interesting evolutionarily to study the distribution of frequencies of generally similar individuals in different populations as a contrast to the more usual procedure of studying the distributions of single characters or genes.

The changes attendant to the general adoption of a "species attitude" such as is outlined above would be few and salutary. Gone from the literature would be the empty discussions of what are or are not "good" species. Systematists could continue to give binomial designations to segregates when they believed that a formal name would be useful. The status of the segregates would be determined by their relationships with other segregates, the relative positions being determined by numerical methods similar to those now being used extensively for studies of groupings at higher levels.

TABLE 2—Q CORRELATION MATRIX—SPECIMEN X SPECIMEN

		2	3	4	5	6	7	8	9	10	11	12	13
SB600	1	.530	.540	.000	—.123	—.090	.311	.101	.499	.472	.423	.423	.376
SB601	2	xxxx	.571	—.050	.077	.031	.496	.424	.594	.649	.305	.536	.572
SB602	3		xxxx	.392	.190	.416	.443	.365	.640	.549	.479	.606	.498
CHAL565	4			xxxx	.603	.642	.229	.378	.220	.103	.248	.160	—.072
CHAL566	5				xxxx	.594	.298	.275	.069	.119	—.022	.067	—.115
CHAL567	6					xxxx	.219	.468	.369	.172	.400	.245	.171
KING8461	7						xxxx	.543	.313	.425	.103	.520	.330
KING579	8							xxxx	.470	.471	.471	.396	.470
WOOD611	9								xxxx	.537	.655	.564	.499
WOOD612	10									xxxx	.431	.580	.588
WOOD613	11										xxxx	.363	.472
MONT6008	12											xxxx	.501
MONT6010	13												xxxx

In summary, I think that the biological species concept has outlived its usefulness. The current revolution in data processing permits the relaxation of the rigid hierarchic system long employed to describe the products of evolution. We may now modify our system to permit more accurate and thus more useful description of the intricate relationships of living organisms. As a step in this direction I suggest that the genetic definition of species, never employed in practice, be discarded as an ideal. Relationships at the lower levels of the taxonomic hierarchy should be expressed numerically, in essentially the same way as relationships of higher categories are now expressed. It is hoped that systematists, as machine methods relieve them of much of their drudgery, will turn more and more to studying organisms in nature. An afternoon of rigorous field observation will usually produce more information of evolutionary value than weeks spent studying preserved material.

I would like to thank the following individuals who kindly took their time to read and comment on this manuscript: H. V. Daly, E. G. Linsley, and R. L. Usinger, University of California, Berkeley; R. W. Holm, G. S. Myers, and J. H. Thomas, Stanford University; A. E. Leviton and C. D. MacNeill, California Academy of Sciences; C. L. Remington, Yale University; P. H. A. Sneath, National Institute for Medical Research, London; and R. R. Sokal, University of Kansas. Many of their suggestions have been incorporated, but the inclusion of their names here does not necessarily indicate agreement with the ideas presented. I am also indebted to Mr. Richard C. Rinkel of the University of Kansas, for using an IBM 650 "Taxon I" program to check the calculations involved in the search for structure in the matrix.

This work has been supported in part by grants G–9821 and G–14740 from the National Science Foundation.

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Phenetic Classification and Typology

HOWELL V. DALY

FUTURE HISTORIANS will doubtless note two technological breakthroughs which have altered the course of systematic biology: the microscope, supplementing the human eye in an age of data-collection, and the electronic computer, supplementing the brain in an age of data-processing. Taxonomists have now agreed that the first step toward biological classification is the gathering of all possible information on the various organisms. This objective is well summarized by Hennig's concept of the "holomorph" (see Kiriakoff, 1959).

The difference in opinions as to how such information is to be utilized stems from the time of Linnaeus. Two approaches to classification are currently recognized (Cain and Harrison, 1960): the phenetic and the phyletic. Classification is the ordering of objects into groups on the basis of certain criteria. In a phenetic classification of organisms, the groups are gauged on an estimate of the degree of overall similarity. The groups of a phyletic classification of organisms are gauged on the relative recency of common ancestry. Both are evolutionary; the phyletic is concerned with the time of divergence and the phenetic system is concerned with the amount of divergence.

Simpson (1961:48) has recently appraised the phenetic methods of Sokal and Michener (1958) and Cain and Harrison (1958) as quantifications of typological procedures. The identification of numerical taxonomy with typology would be of little consequence were it not that classical typology has gained the connotations of metaphysical, dogmatic, or anti-evolutionary thinking. To understand Simpson's meaning, I would like to quote the following (1961:46–47): "The basic concept of typology is this: every natural group of organisms, hence every natural taxon in classification, has an invariant, generalized or idealized pattern shared by all members of the group." In the terms of Aristotelian logic at least one character or *fundamentum* must be common to every member of the group. Beckner (1959) has referred to this concept as "monotypic." His use of this word should not be confused with its customary meaning among taxonomists, that is, a taxon T_{j+1} with but one T_j. The conceptual companion to a monotypic group has been posed by Beckner as a "polytypic" group or aggregation. Simpson (1961:94) has paraphrased the terms of such an aggregation as follows:

"1. Each individual has a large but unspecified number of a set of properties occurring in the aggregate as a whole.

2. Each of those properties is possessed by large numbers of those individuals.
3. No one of those properties is possessed by every individual in the aggregate."

The application of the polytypic concept to the products of organic evolution is clear. The basis for Simpson's reluctant view of numerical taxonomy is that these methods impose the monotypic concept of classical typology on groups of organisms which are empirically polytypic. I believe this is incorrect and I would like to support my objection by placing both methods in a historical perspective.

An ambitious synthesis of natural phenomena must inevitably encounter polytypic categories. No doubt exists that Plato and Aristotle were aware of natural variability. Order, however, was pursued in spite of variability by the proposition of monotypic classes established by strict rules for classification. The typology of Aristotle can be traced through the scholastics and Thomistic philosophy to the next landmark, the Linnean system. Cain (1958) has shown that Linnaeus intended to follow the Aristotelian rules for logical division in the separation of species in a genus. The need for a common character, together with an idea of what are the important characters, necessarily discouraged polytypic descriptions.

Among the natural philosophers of the eighteenth century, Goethe was one of the first to be occupied with the details of nature and one of the last to indulge his imagination. The type concept of his morphology was developed as a practical means for unifying the variation in plant and animal anatomy. The comparison, character by character, over a large number of organisms was considered to offer no possibility for unification. An animal type was created by contemplation which would embody the general image of the forms of all animals and to which all could be compared. As a corollary, no single animal could be the model for all others (Hall, 1951). Although his mental abilities were unusual, he never produced a description of the type.

In France, Cuvier formulated a type or ground-plan for each of four groups of animals. To define these types, he sought to methodically discover the important or dominant characters which either influence all others or are constant throughout a series. Animals within a group could be compared to the ground-plan, but no speculation was allowed on the possible similarities between ground-plans. This disapproval of conjecture marked him as one of the first empirists (Cain, 1959). Owen, the English anatomist, built into Cuvier's methodology a distinction between analogous structures, similar in function, and homologous structures possessing essential similarity. The determination of essence was apparently performed in the same fashion as the formulation of ground-plans, that is, by an intuitive synthesis.

With the appearance of Darwin's theory of evolution, the fundamental or important characters of Cuvier's classification were replaced by a selection of those features least likely to be modified by descent. Structures possessing essential similarity were reinterpreted as structures similar because of inheritance from a common ancestor.

We may now ask if the phyletic approach can deal with polytypy? A brief example of a polytypic aggregation is as follows: $T_{j,1}$ (characters a, b, c), $T_{j,2}$ (characters b, c, d), and $T_{j,3}$ (characters c, d, e). The condition of interest here is the absence of a homologous character, such as b or d, common to every T_j. According to Simpson (1961:95) the aggregation or T_{j+1} is a valid phylogenetic taxon since each successive pair can be defined monotypically by the presence of at least one common character. To show recency of common ancestry, however, it is necessary to violate the polytypic concept. At least one character in its most recent evolutionary form must be common to each member of the contemporaneous aggregation to make phyletic comparisons. This has been ex-

pressed by Simpson (1961:96) as follows: "For consideration of any one ancestral character, the sequence involved as evidence must of course have a single *fundamentum* . . ." (italics his). To circumvent this difficulty with fully polytypic aggregations, the phylogeneticist renders a judgment on the probable relationship based on the various lines of inference at hand.

It is now clear that the phyletic approach has perpetuated the most undesirable attributes of classical typology: the need for a fundamental character and the intervention of personal judgment in the event none can be discovered. To treat the problem of polytypy and to reduce the influence of the individual investigator, our attention must now return to the time of Linnaeus.

In reaction to the selection of a few *fundamenta,* the French botanist Adanson (1763) insisted on using every part of a plant and giving each feature equal weight. His method was to prepare separate classifications of the same plants, each based on a different part. The final classification represented the general coincidence of the groups of the preliminary studies. This was the first purely empirical approach to classification.

In the same year as the publication of Adanson's classification, 1763, a landmark appeared in another discipline, statistical probability. This was the essay, published posthumously, by the Rev. Thomas Bayes (see Deming, 1940). His manuscript took the first step toward using the theory of probability as a means for reasoning from the particular to the general. In the absence of definite knowledge, Bayes took the position that all probabilities should be equal. This postulate has since been rejected on the grounds no probability should be assigned *a priori.* Statistical methods are now devised so this uncertainty can be evaluated.

The application of numerical methods to samples of many characters provides a way to classify polytypic aggregations at any level. The general procedure is quite simple. A number of T_js are each examined and measured or scored for a large number of characters. Each T_j is compared with every other T_j on the basis of the characters which are common to each pair of T_js. The degree of association between each pair is estimated by a suitable index. On the basis of these indices, groups of phenetically related T_js are formed into a hierarchy by one of several techniques. The final result can be presented as a dendrogram of phenetic relationships.

The characters used for any one study are only a portion of many possible characters. It is a working hypothesis that different collections of characters from the same initial T_js should give indices of association which are closely similar in magnitude. Ehrlich has given a test of this hypothesis in this symposium. A phenetic classification which is demonstrated to be invariant regardless of the selection of characters is independent of the need for *fundamenta.*

Ehrlich's present study, as well as that of Sokal and Michener (1958), is an analysis of characters present in each initial unit. Fully polytypic aggregations would possess no common characters. Several techniques are now available (Cain and Harrison, 1958; Rogers and Tanimoto, 1960; Sokal, 1961) which allow the analysis of such data.

In conclusion, an obvious parallel can be drawn between the histories of taxonomy and psychology. In the last century many types of personalities were promulgated on the basis of circumstantial evidence and imagination. That these types could rarely be recognized with certainty led to the application of statistical techniques. Later, the preconceived types were abandoned altogether and the numerical methods became used not only for description but also for the discovery of types. The new typology of taxonomy, as in psychology, no longer depends on the unique experience and the unwritten notions of the investigator, but on an

analysis of observations open to scrutiny at every step.

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Man Versus Machine: A Future Problem in Protozoan Taxonomy[1]

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THIS PAPER concerns the application of computers to taxonomy. The word "future" is included in the title because the speaker does not at present know a single full time taxonomist who is interested in the application of computers as described below. Evidence that this deficiency exists on a national scale can be seen in the contents of a report on the use of computers in biological and medical research (Ledley, 1959) now being prepared by the National Academy of Sciences—National Research Council. The subject of taxonomy probably will be omitted because the organizing committee could not find a taxonomist interested enough to write that section.

The word "protozoan" in the title of this paper is used in its broadest sense. My favorite definition of the Protozoa simply states that the Protozoa consist of all organisms that might conceivably include a one-celled stage in their life history (Jahn, 1955). By using this definition I will have sufficient scope to discuss all of the principles that time will permit, and I will bow slightly toward conventional taxonomy by drawing most of my examples from those organisms that other taxonomists include among the Protozoa.

If we examine the possible use of computers for taxonomic purposes we can make certain predictions concerning this use. Some of these predictions are:

(1) That we could save a considerable amount of time and a larger amount of confusion for investigators and

[1] An outgrowth of experimental work supported by NIH RG-6462 and ONR Contract 233 (65).

for students by the use of numbers as well as names for all taxa, and even by the substitution of numbers for names in many technical discussions,

(2) That the most efficient use of computers would require a completely logical taxonomic system,

(3) That the development of a completely logical system will require some severe revisions of our present system,

(4) That names, although still used, will become less important,

(5) That the laws of priority will decrease in importance along with the names, and might eventually be discarded,

(6) That the development of the currently booming field of taxonomic jurisprudence will be inhibited,

(7) That all of these developments will irritate most taxonomists,

(8) That the taxonomists will rise to fight the machines,

(9) That the machines have already started the battle (a *post facto* prediction),

(10) That the machines will win, whether the taxonomists fight or not,

(11) That the proper progressive move for taxonomists is to revise the present system so that machines can be used to the advantage of taxonomy,

(12) That such a revision would be an improvement, even if we did not have any machines, and

(13) That a logical revision of the present system to fit the age of machines will necessitate intensive research on the taxonomic characteristics of many organisms and could result in a great increase in our knowledge of biology.

The coding of biological data for analysis by computers was first attempted by the OSRD project of the Chemical-Biological Coordinating Center (CBCC) which screened anti-malarials during World War II. The system then used has recently been published (Seitner, Livingston, and Williams, 1960; Seitner, 1960). The taxonomic portion of this code is limited in function to a filing system, with the categories based on the taxa found in standard reference works. For instance, *Plasmodium hexamerium* is given the number 1310101D. This means that the organism is placed in the Phylum Protozoa (1), Class Sporozoa (13), Family Plasmodiidae (13101), Genus *Plasmodium* (1310101), and is species D. *Plasmodium praecox* has the same number except that it is species C, and *P. relictum* is species 9, with the number 13101019. *Amoeba proteus,* along with its supposed synonyms of *Chaos diffluens* and *Amiba diffluens,* is assigned the number 11101011. Various chemicals used were given numbers already established in the compatible Chemical Code. Various physiological effects, the conditions of the experiment, etc., were given numbers in accordance with the Biology Code. The computer was able to produce required information on the existence and possible correlation between any number of the total of over 220,000 items stored in its memory. In so doing it served many very valuable experimental functions.

The CBCC system could be revised to accommodate as many taxonomic levels as we need. At present we have about twenty commonly used levels in the modern hierarchy of classification between the kingdom and the subspecies. If all possible super-, sub-, and infra-levels were used the total would be thirty-four, probably more than ever needed in practice (Simpson, 1961; 17). Any number of levels could be indicated by an appropriate series of numbers, one for each level.

Such a system could easily be expanded to include life on other planets, even if these non-Earthian organisms were to have chemical compositions based primarily on silicon, nitrogen, or some other element in place of carbon; one more digit

in the code number could accommodate eight or even 34 non-Earthian systems.

However, there are much more economical ways of using part of the total of 80 columns on a standard IBM card. If we are going to use the card for filing of descriptions, experimental data, etc., we should leave most of the columns available for that purpose.

A standard card has 12 positions in each of the 80 columns, 9 digit positions (1 to 9) and three zone positions (called 12, 11, and 0). The two groups can be used singly or in combination to denote the letters A to Z. Each column, using 1-9 and A-Z, with no zone punches used alone, yields 35 combinations. This could be increased to 38 by using the zone punches alone. Additional columns would add a power of 35 or 38. Therefore, if the zone punches used alone were retained for other purposes,

2 columns would yield 1,225,
3 columns would yield 42,875,
4 columns would yield 1,500,625,
5 columns would yield 52,521,875,
6 columns would yield 1,838,265,625, and
7 columns would yield 64,339,296,875.

This is more than enough numbers to classify all known species, subspecies, and strains, even allowing for use of only a fraction of the possible combinations.

By using two columns for species, subspecies, and races (maximum of 1225 for each genus), one for genera (maximum of 35 genera for each family), one for the family (maximum of 35 families for each order), and grouping the higher taxa without having a separate column for each, we could provide a code for over 60 billion species, subspecies, races, and strains, with only 7 alphanumeric digits. One or two hyphens could be used to separate higher from lower taxa at any point or points desired. In this way each strain of each species would be designated by a maximum of seven symbols, such as 4C7-6M-X5. This group of symbols would distinguish it from all other known organisms, and furthermore would describe its classification completely. By using a total of nine digits we could provide separate digits for kingdom, phylum, class, order, family, and species. With eleven digits we could do this and also increase the possible number of genera per family to 1225 and also the number of families per order to 1225. This seems like a larger system than we need, and one with fewer digits may be preferable.

One interesting consideration is that certain combinations would be excluded because the letters involved might be pornographic or otherwise undesirable. However, the techniques of overcoming this problem already have been worked out by the state departments of motor vehicles in the assignment of automobile license numbers, and their lists of unacceptable combinations might possibly be available to authorized taxonomists.

It should be noted that each level does not need to appear in the code number. If we have less than 35 phyla for all kingdoms, the kingdom could be omitted and the first digit would represent the phylum.. For instance, if phyla 1-3 represented viruses; 4-6, bacteria; 7-9, fungi; A-C, protista (protozoa and unicellular algae); D-K, plants; and L-Z, animals, or if we had some other comparable system, the kingdom would be implied automatically by the code for the phylum. The same could be done for lower taxa.

It also would be possible to go one step farther and to eliminate the names "kingdom," "phylum," "class," etc., and to speak of "level I," "level 2," "level 3," etc. The level could be the number of the digit or the digit pair that is used in the code number. Consequently, we could speak of mammologists as experts on group T2X-Mammalia, or simply on T2X, or whatever the code number for the mammals might be, rather than as experts on the Class Mammalia. This would avoid whatever psychological disadvantages are caused by the use of terms such as kingdom, superclass, infraclass, cohort, subfamily, etc., the special meanings of which are unique

to the system and have to be learned by each student. It would be interesting to know how many students remember where "cohort" and "tribe" belong in the hierarchy after they have passed a final examination. However, all of the students know that level 8 is between levels 7 and 9, and this is something very few will forget.

The system described by Denmark, Weems, and Taylor (1958) uses 16 digits of numerals only. Their system is an open ended one, with numbers for each taxonomic group assigned at random. Each species has a permanent number, and these numbers may be rearranged in any type of regrouping desired. However, the number does not automatically describe the classification of the organism. This system seems excellent for a filing system, as intended by its inventors, but it definitely is not a coded taxonomic scheme as suggested in the present paper.

The ultimate of ultimates in a machine code for taxonomy would be a translation of the code of the DNA in each chromosome. If and when this should become possible the code number would be a complete description from the genetic viewpoint. If such a code were placed on present day cards or tape it would necessarily be very much larger than the DNA code which requires only three purine or pyrimidine residues for each amino acid (Levinthal, 1959). I have heard estimates that the code of the 46 chromosomes of man, if set in type, would fill a thousand standard books. Some of our larger mammals, led by the sulfur bottom whale, would be larger than the code, but most organisms would be smaller. Other coding techniques are more compact. Possibly an exact and periodic comparison of the relative sizes of machine code and organism DNA code might be used as an index of our progress in the field of microcoding techniques, with the engineers vainly striving to achieve a code as compact as that of DNA. This would be one contest where I would bet on the organism.

If we should ever achieve the complete duplication of the DNA code, regardless of the compactness of the machine code used, the code for any given virus might serve as an indication of whether the virus was left over from the primordial organic soup which preceeded the existence of cellular organisms or whether it is, or was descended from, a fragment of a modern chromosome.

As far as taxonomy was concerned the computer used by CBCC was merely a cross reference filing system, ready to divulge all of its information about any organism upon request. The expansion of the code suggested above would not change the limitation on the function of the computer. The same purpose can be served on a smaller scale by a set of edge-clipped punched cards of the type that can be sorted manually by means of an ice pick (Casey and Perry, 1951; Levine, 1955). A cross reference filing system serves a very useful function. However, any computer limited to this function is 20 years out of date, and in the field of computers anything 20 years out of date is practically prehistoric.

The question which then arises is "How can modern machines be used to best advantage in taxonomy?" For instance, could we code a complete description of an organism on a card, drop it into a machine, and have the machine tell us its proper name and code number? Or if it is a new species what its number should be, and what characteristics might be used in forming a new name? Or what the name should be, with the new name given correctly, to suit the sensitive taste of the professors of classics in regard to the proper language and grammatical correctness? The new code number, of course, would tell automatically the complete classification of the organism.

Furthermore, the machine could be instructed to question the operator before it accepted a species as new. It might say "This organism has never been described before. Does it really exist? Are you sure

you punched holes only in all the proper places?" Or "Congratulations! You have discovered a new phylum." Or "Why don't you take a course in hole punching?" Or something witty.

The above task would be easy for any moderate sized computer and actually could be handled by a relatively simple machine. The only requirement would be that we teach the machine the method of classification to be used. This "teaching" could consist of feeding it a piece of magnetic tape on which we had coded either the whole taxonomic system or some suitable section of it depending upon the scope of the taxonomic work being done and the size of the machine. Presumably these tapes would be available in suitable taxonomic units from any good biological supply house, and we could avoid overtaxing the memory of a small machine by feeding it only the sections needed, and store the others on a shelf. With modern computer techniques these things, and many more, are possible.

The next step is to teach the machine how to classify unknown organisms. If we had a completely logical system of classification this would be automatic, because the machines are inherently completely logical, and a logical classification could be coded by the machine directly from the description. However, our classification is *not* completely logical, and some portions of it are highly illogical.

Machines can *not* think illogically; their logic is infallible. They even have an automatic system (known as "bundling") to prevent errors due to faulty components. They can be taught to arrive at illogical conclusions, but only if we give them specific instructions not to obey the rules under certain conditions. Numerous investigators are now trying to design machines to duplicate activities of the whole brain (e.g., WADD; NPL Symp. 10). Presumably such a machine could even be programmed to yield any given percentage of inconsistent conclusions, either concentrated in one area of its activities or completely at random, thereby simulating a wide variety of human minds.

Therefore, by feeding the machine enough instructions on when to break the rules, it should be possible to teach them to classify any organism in exactly the same way that the organism would be classified in the mind of a taxonomist. Such an accomplishment undoubtedly would have to be acknowledged as an advance in the new science of bionics (the use of organisms as prototypes of electronic devices). It might even be considered an advance in the science of intellectronics. However, regardless of how great a technical advance this might be considered, it is an achievement that is not flattering to those of us who like to regard the human race as rational and even hope that it will become more rational.

Furthermore, the goal to be achieved by intellectronics is not to copy human errors of thought, but to serve as an extension of man's intellect. This goal, as stated by a leading firm of engineering consultants (Ramo-Wooldridge, Intellectronics Division) "is to achieve a synthetic intelligence, part human and part mechanical, which combines the strongest features of both, to produce a new order of intellectual power exceeding that of either men or machines operating separately." (Physics Today, March, 1961, back cover).

In teaching a machine how to classify organisms illogically we would not be making the best use of its abilities; in fact we would be discounting one of its primary virtues.

Apparently it will soon be possible to give a machine a heuristic program instead of specific instructions, and to teach it how to classify organisms illogically by a trial and error, reward and punishment method (WADD; NPL Symp. 10), very much like that now used for the training of human taxonomists. This also would be a great technical achieve-

ment, but is it one we should encourage?

For example, why should we teach a machine that thousands of species of unicellular marine organisms with fancy skeletons and filipodia, but without axopodia at any stage in their life history, should be classified as Radiolarida, whereas in defining the Actinopodea in which the Radiolarida are included we separate all of the Actinopodea from the Rhizopodea on the basis of the presence or absence of axopodia, and state that axopodia are present in the Actinopodea (Jahn and Jahn, 1949; Hall, 1953; Kudo, 1954, and all other standard texts and monographs)?

To me it would seem embarrassing to tell a highly logical machine to retain this illogical dichotomy because:

1. The mistake has been in existence for about a hundred years,
2. In a recent monograph (Trégouboff, 1953), this irregularity was mentioned but not corrected,
3. The Committee on Taxonomy of the Society of Protozoologists, at a meeting at Stillwater in 1960, refused to make the necessary corrections, even after the gross inconsistency of the dichotomy was pointed out and corrective measures were proposed (Jahn, Bovee, and Small, 1960) at a symposium held for the purpose of examining the current taxonomic system prior to revision.
4. Most people who write about the Radiolarida do not examine living specimens.

Similarly, should we tell the machine to classify large non-chlorophyll-bearing ameboid organisms (Mycetozoida) as plants? If we do we might have to give the following reasons:

1. Most people call the Mycetozoida "slime molds."
2. Most of the people who have worked on the Mycetozoida call themselves "botanists."
3. The Mycetozoida were classified as plants in 1829 A.D.
4. One distinguished botanist, De Bary, on the basis of good evidence, separated them from the plants in 1858, but was ignored by the botanists.
5. They form complicated masses of gametes, sometimes called "fruiting bodies."
6. They live on decaying wood.

The machine might answer back that common names are meaningless, that errors of the past should be corrected, that some snails lay complicated egg masses, and that some Mycetozoida like to eat oatmeal and bananas.

Confusion and illogical dichotomies are by no means limited to the Protozoa, and the existence of illogical separations is recognized by investigators of other groups. For instance, Sneath (1957b) states "bacterial classification is in such confusion that it seems doubtful whether any nonsense can make it much worse than it is."

Our usual method of separating plants from animals is also illogical. We would have to teach the machine that we separate plants from animals primarily on the basis of the presence of chlorophyll in plants, but that we (not I, but at least most of us) also ordinarily place the bacteria, fungi, and possibly viruses in the plant kingdom. Would it not be much more logical to define plants in such a way as to include only those organisms with green chlorophyll and then to have separate kingdoms for the bacteria, fungi, viruses, and possibly all nucleated unicellular organisms, as well as for animals? Then we would have to teach the machine only a very small number of exceptions. An example of an exception would be the snowplant (*Sarcodes sanguinea*), and for this exception we could give reasons acceptable even to a highly logical machine.

For easiest handling by machine the separations of the taxa used should be based on mutually exclusive, and preferably single unit dichotomies. The same statement is also true for the old-fashioned methods of taxonomy now in use; the in-

troduction of as many mutually exclusive single unit dichotomies as possible would be an improvement in the system, both logically and phylogenetically. Our present taxonomic system has been planned on the basis of serving two primary objectives, namely, 1) to function as a filing system, and 2) to serve as the basis of a phyletic tree, especially when fossil forms are included. The latter function must necessarily always be incomplete because so many organisms are no longer available, even as fossils. However, if we assume that in the past most mutations arose, or at least survived, single, as they do today, then all or almost all dichotomies would be based originally on single mutually exclusive characters. This should be obvious if we could examine simultaneously all of the organisms whose descendents are alive today. For the forms now available for study, some dichotomies must consist of multiple units, such as possession or absence of characters A, B, C, *and* D, but the separation would still be dichotomous and mutually exclusive. This does not mean that we can have only two sub-units of equal rank in each unit; the actual number could be unlimited, as at present.

It might be pointed out that the use of a rigorous A:not-A dichotomy as proposed here may often be inappropriate in dealing with currently evolving organisms (Simpson, 1961; 22) and would tend to lead to artificial or arbitrary classifications. Complete dichotomies can encounter all of the objections applied by Simpson (1961) to symbolic logic or set theory as used by Woodger (1952), Gregg (1954), and Beckner (1959). Moreover, since the primary process involved in symbolic logic, namely logic, is characteristic of machine coding, there is no way to circumvent these disadvantages. In view of the obvious fact that many closely related species overlap in some or even all of their characters it is impossible to expect a universal or even a very widespread use of mutually exclusive characters for specific differentiation. However, for higher taxa, between which the evolutionary gaps are wider, the taxonomic lines are or should be more clear cut.

It should also be possible to formulate a numbering system for plant species which are known to be hybrids of other well known species, e.g., in the genus *Clarkia* (Lewis and Lewis, 1955). These are special cases which would require special treatment under any taxonomic system. Possibly the same problem exists in animal taxonomy.

In some of the lower taxa, where species and varieties overlap in most of the characters which are used to distinguish them, and are definable only on a statistical basis (e.g., Stroud, 1953; Cain and Harrison, 1958, 1960), pioneer work along the line of having computers perform multifactor analyses has been done (Sneath 1957a, 1957b; Rogers and Tanimoto, 1960) and should be continued. One primary advantage of using computers for this purpose is that the taxonomist must formulate the criteria for the decision in logical terms before he can tell the computer how to make the decision. This application of computers merely substitutes machine-computed numbers for the value-judgment of the taxonomist, and is not necessarily opposed to the idea that we should strive for mutually exclusive criteria. Whenever it is not possible to separate certain groups on the basis of mutually exclusive criteria we can then instruct the machine to use the multifactor analytical methods. This is one of the methods now being developed for the machine-handling of what engineers refer to as "soft" data. In this sense "soft" means incomplete or inconsistent, and it can be applied to a variety of biological data, including medical statistics, a field which is even more inconsistent than taxonomy.

Introduction of a completely (or almost completely) logical system, with mostly mutually exclusive dichotomous criteria for separation of taxa, would involve a

thorough revision of our present taxonomic system. We could start by adopting a half dozen kingdoms. Multikingdom systems have been proposed by Copeland (1938, 1947), Jahn and Jahn (1949), Whittaker (1959), and others.

The system below is silghtly modified from Jahn and Jahn (1949):

1. ARCHETISTA (Viruses). Submicroscopic, living in animals, plants, or bacteria in which they cause diseases, e.g., poliomyelitis, mumps, tobacco mosaic disease, and bacterial lysogeny.
2. MONERA. Without nuclei, cells solitary or physiologically independent. Bacteria, blue-green algae, and spirochetes.
3. PROTISTA. Largely unicellular, with nuclei. Protozoa, green algae, red algae, and brown algae.
4. FUNGI. Usually numerous nuclei; contain no chlorophyll; in many species cell walls do not separate the cytoplasm into typical mononucleate cells; usually sessile.
5. METAPHYTA or EMBRYOPHYTA. With chlorophyll; multicellular; usually sessile.
6. METAZOA. Multicellular; typically holozoic; usually motile.

Another possibility would be to delete the Protista and divide these organisms on the basis of possession (present or recent) of chlorophyll and distribute them among the fifth and sixth kingdoms, which would then be redefined and renamed as plants and animals. We also could place the blue-green algae in the same group as the plants. These changes would yield the following kingdoms:

1. Viruses
2. Bacteria (including spirochaetes)
3. Fungi
4. Plants
5. Animals

In this system the green flagellates would be plants, and because of my research interests I would autómatically become a botanist as well as a zoologist. Conversely, my very good friend George W. Martin, Professor Emeritus of Botany of the State University of Iowa, and a world authority on the Mycetozoida, would become a zoologist as well as a botanist.

The use of common instead of Latin names might hasten acceptance of the above or some similar scheme. It is possible that one reason the system of Copeland or of Jahn and Jahn has not been generally adapted is that new names bother people. So do very old names that have not been used for generations and for which priority is claimed. However, names are relatively unimportant compared to the ideas, and the names would become even less important if combined with a number. For example, in Los Angeles we know that the telephone exchange GR is Granite, but this information is really not essential, even for calling a number orally, and is completely superfluous if we use the dial. Similarly the Kingdom Bacteria could become 2-Bacteria. The name only would be used in conversation by non-specialists. The machine could be told to print out the name as well as the number when preparing reports for non-specialists. However, as far as functioning of the machine is concerned, only the number 2 is necessary, plus the information that 2 is the first and only digit.

The substitution of numbers for names as described above is essentially what has happened in astronomy. The names for the stars and the constellations are useful for amateurs and also for casual conversations among professionals, especially with laymen. However, all records are kept by numbers, and names are seldom used in serious discussions by professional astronomers, many of whom do not know the names for more than a couple of dozen. The relative number of known stars and of known species or varieties of organisms depends upon the size of our telescopes, and the industriousness of

astronomers on one side, and the number of methods used for biological observation, and the industriousness of our taxonomic "splitters" on the other. The stars now outnumber the species. However, the number of described taxonomic varieties is now so great that computers could well be used for cataloging the data, just as they are used in astronomy.

If the name of a taxonomic group is not necessary for the machine, is it important which of several synonyms is used? For instance, we can teach the machine all of the 30 synonyms that have been used for the Foraminiferida or the 45 synonyms for the Order Proteomyxida, the 59 synonyms for the Superfamily Trichiacea of the Mycetozoida or the 45 synonyms for the Order Mycetozoida. All of these have been carefully and accurately compiled by Loeblich and Tappan (1961). We could instruct the machine to type out the whole list whenever requested or even whenever the group is mentioned. Otherwise, we could instruct the machine to use one and only one of these names, and to translate all synonyms which it might receive into the one name designated. However, some of the synonyms have also been used as synonyms for other currently recognized taxa, and we would have to teach the machine how to distinguish these various meanings. For the primary purposes of serving both as a filing system and as a record of phylogeny these other names are useless burdens. The only thing of importance to the machine is the number. Therefore, for efficient use of the machine all of the synonyms could be placed on a separate tape and placed in storage. The machine could be told to remember only one name and to use only that one name when speaking to non-specialists.

If this is done, does it matter which name is used? Only for historical purposes, and to create a memorial to the first person to use the name as applied to the group being discussed. As far as the advancement of science is concerned the important thing is the definition of the group included under the number. On this basis the currently booming field of what I like to term "taxonomic jurisprudence," namely the determination of the proper name for each taxonomic group, becomes not only less important, but virtually useless. The current boom is caused by the ruling that the laws of priority, formerly applied only to genera and species, should be applied to families. There is now a movement to extend this application to the higher taxa either gradually or as rapidly as possible. This should supply future work for the taxonomic lawyers for a long time, whereas introduction of the numerical system might tend toward a condition of technological unemployment. Simpson (1961:34) refers to legalistic nomenclature as "a necessary evil taking begrudged time from more important matters." It seems to me that the word "necessary" in this statement should be changed to "unnecessary."

An outstanding example of how strict attention to historical precedent has hindered the development of a logical system is found in the papers of Copeland (1938, 1947) mentioned above. Copeland's conclusions regarding the proper legal name for each kingdom are well documented, and are in accordance with the rules of priority. Moreover, it is obvious from his discussions that as long as the historical perspective and the rules of priority are retained it will not be possible to obtain a logical set of dichotomies even for the kingdoms.

One of the best things that can be said about the arguments concerning validity of names is that these discussions may stimulate more interest in the characteristics of the organisms.

Introduction of the logical system as demanded by the machine would more than ameliorate the technological unemployment situation because taxonomists would be needed to revise the present system to meet the logical standards of

the machine. Furthermore, in order to place the system on a logical basis we will need to have much more information about many organisms. The problem of obtaining such information will require the concerted effort of so many taxonomists that the threat of technological unemployment might well be converted into a shortage of trained personnel. Therefore, the effort now devoted to determination of which name is valid might be better spent in learning more about the organisms and the dichotomies to be used.

For instance, in the field of ciliate protozoan taxonomy, Corliss (1956) has advocated that the patterns of adult infraciliature be used as the basis for suprageneric ciliate taxonomy. However, at present we do not have the infraciliature patterns of 21 of the 34 genera of the present family Frontoniidae. This is true in spite of the fact that there are about 50 professional and graduate students who have a taxonomic interest in the family. If we accept Corliss' suggestion we can decide how to classify these 21 genera only after we obtain the necessary information about their infraciliature.

Possibly we should suggest some sort of International Taxonomic Year, comparable to the International Geophysical Year. During the ITY we could try to revise our system. It is highly questionable whether this could be done in a year; a decade or a century would be more appropriate. However, in a decade the machines, if unopposed, will already be using another system.

In regard to the introduction of a logical system one thing seems certain. If the taxonomists do not undertake this job, the professional "programmers" trained in mathematics, logic, or the philosophy of machines, but not trained as biologists, *will* do the job. If so, they will invent a completely logical but highly arbitrary system that may have no relationship to phylogeny.

Once such a system is invented and is in use by the machines, the biologists will be forced to use it, regardless of whether a phylogenetic system is retained for other purposes. The reason for this is that some literature is already being indexed by machines in chemistry, physics, and physiology. All of these sciences use organisms, at least to some extent, and if the machines are going to classify the data they must have numbers for the organisms. If necessary, the numbers will be assigned by a person who is not a biologist and the numbers may not fit into any biologically logical system. However, the biologists then will have to learn to use this arbitrary system. At the rate scientific papers are being published any system introduced probably could not be changed because the cost of recoding all existing literature will be too great. Compared to such an undertaking the problem of changing the cataloging of a million book library from the Dewey decimal system to that of the Library of Congress would be very simple. The library indexes only the volumes, whereas the computers will index the *contents* of each paper.

The present state of affairs is represented by *Chemical Titles* and *Chemical Patents* which are two cross indexed lists published by *Chemical Abstracts*. These are now prepared completely by machine from the tables of contents of the publications covered (Dyson, 1961). The next step might be to have machines print key phrases from the author's summary and then eventually to print these instead of the abstracts.

Another possibility is to have the author code the essential results on a standard code sheet, to have this checked by a professional coder employed by the editorial office, and to have a properly punched IBM card reproduced in the journal in which the paper is published, or made available from an international card distributing service. These cards could be used directly or copied by libraries on microfilm, Minicards, magnetic tape or any other type of storage medium.

With such a system available it would be an easy matter to obtain a printed list, for example, of all known effects of temperature, of salinity, or of drug X76-504-329 on organism 543-71Z-M15 and its relatives, or of related drugs on other related or non-related compounds, etc. If such a system were adopted in large libraries or on a national or international scale it could eventually replace most of our indexing and abstracting journals and save much of the time now spent in searching for literature. In some instances it is already easier and cheaper to repeat certain investigations than it is to find out whether it has been done before, who did it, where the paper is published, and to obtain a copy, and the problem is continually getting worse as each new journal is announced.

It seems fairly certain that any taxonomic system used for the first really large scale indexing of biological literature will automatically become *the* system of taxonomy, frozen by the fact that it will have permeated so much of the machine-indexed literature that changes will be impractical.

It is for this reason that I suggest that the taxonomists should revise the present system as rapidly as possible, in such a manner that it will be logical, and at the same time representative of phylogenetic relationships insofar as possible. This suggestion is made in the hope that when the system is frozen, it will be the best system we can produce at the time.

If the taxonomists wait until this freeze occurs and then develop a logical system there will be two systems, one for the general biological literature, and another for the organisms and for the taxonomic literature. This may happen in spite of any efforts we might make. We can only hope that if this occurs some system of machine translation can be perfected so that our taxonomic troubles will not be doubled.

Machine translators are now being developed to translate not only languages (Delavenay, 1960) but also codes and programs from one type of computer (i.e., analog or digital) to the other or to a hybrid (Kent, 1960; Paskman, 1961) or even from one commercial brand of computer to another. Presumably the phyletic system will be subject to continual change as long as taxonomic research continues. Therefore, it is possible that eventually we may have machines to translate the phyletic system that is current at any future time, into the completely arbitrary system that probably will be developed within the next five years.

The existence of two systems can be quite confusing, and we already have two systems for some groups, e.g., the Suctoria. We have a practical or arbitrary system based on the characters which one can see by looking at the organism, and a phyletic system based on the method of reproduction (which one usually does not see) for the major dichotomies and on structure for the minor dichotomies (Kahl, 1934). Any novice who has tried to learn how to classify a suctorian knows how confusing this system can be. Some years ago Goodrich and I (Goodrich and Jahn, 1943) found internal budding in only six of several hundred specimens of a new genus examined. These six specimens were found during the last of fifteen weeks during which we made our observations. If we had not worked that last week we would have placed a new genus in the wrong family. This type of situation exists in many groups, and as Bigelow (1956) pointed out, the arbitrary and phyletic schemes are not necessarily compatible. More often they are not compatible. Furthermore, at present we do not seem to be able to obtain help from the machine toward a solution.

An alternative to letting a professional programmer work out a system is to ask the machine to do it. Perhaps this is the method that most professional programmers would prefer, and it has been used for bacteria by Sneath and Cowan (1958). The machine was given complete descrip-

tions, told to consider every feature of equal importance, and asked to classify the organisms on the basis of overall similarity. As might be expected, the machine-made classification shows both similarities and differences when compared to the one now in use. In general, which of two systems derived in this manner is better will depend upon how much information is given to the machine and on how logical the taxonomists have been. One basic idea among taxonomists is that certain characters are more important than others. Unless the machine is so instructed we should not expect the two systems to be the same.

A movement in the direction of a completely logical system will restrict the expanding application of the laws of priority, and to most taxonomists this is anathema. However, in the universe as it currently exists, the really important item is the code number. This fact was emphasized to me some time ago when I received a new research grant which I knew had been properly received and approved by the Regents of our University. I knew the amount, the granting agency, the purpose of the grant, the official title of the grant, the name of the head of the division of the granting agency, the reason he had reduced the amount by two %, the name of the division, the starting date, the closing date, and much other pertinent information. However, for some time I could not spend any of the money because someone had failed to assign any code numbers. No requisition can be processed without a code number. The same may soon be true of new species. Possibly the proper coding for a punch card will be required for all new species, just as a description in Latin is now required for new species of plants.

In order to minimize any misunderstandings in regard to my reasons for presenting the present discussion, I wish to state that the purpose of the present paper is *not* to try to sell the use of machine coding to taxonomists. Furthermore, I am not saying that machine coding is better than our present system or that we should adopt it. One reason I am not making these statements is merely that I am not interested in jousting with windmills. However, as an interested spectator I do wish to point out that unless the windmills stand aside they will be overwhelmed by the machines. Furthermore, one humiliating item is that the machines that will overwhelm the windmills will not be enormous monsters bearing the insignia Remington-Rand-LARC, IBM-7090, Philco-2000, CDC-1604, Burroughs-5000, or any other insigne designating the current personification of machine perfection, but merely some of the primitive ancestors or near ancestors of these magnificent creatures, possibly some very modest models that already have been available for years and are now outmoded for high speed calculation because of the rapid advances in solid state physics and microelectronics.

In brief, I wish to point out that the use of machines will be forced upon us by the progress of civilization. Therefore, it behooves us to make our taxonomic system as logical as possible and as phyletically correct as possible *before* the system is stabilized by the inertia of millions of standard punched cards and Minicards and of megamiles of magnetic tape, punched tape, microfilm, and other possible storage media.

I do not mean to infer that taxonomy is the only field of biology in which illogical dogma is handed on to students, one generation after another. For example, the writers of most of our textbooks discuss mother cells and daughter cells in the somatic lineage of higher organisms of both sexes and of unicellular organisms that are not known to even have any sexual phenomena (e.g., *Euglena*), whereas they really mean parent cell and filial cell. Furthermore, they almost invariably discuss conjugation as a method of sexual reproduction in *Paramecium*, even though it is well known that conjugation is

merely a temporary union of cells for the exchange of nuclear material and is not at all a method of reproduction. I have pointed out these obvious inconsistencies previously (Jahn and Jahn, 1949), but I have not detected any great rush on the part of textbook writers to correct them. Doubtless many other such illogical definitions exist in the literature. The worst thing about the existence of these definitions is that they give students illogical concepts and confusing habits of thought. It is for this reason, as much as for lack of information, that the field of biology has not been developed into coherent science. Now we are rapidly accumulating more information in all fields of biology, and in order to make best use of this information, we need to eliminate the logical inconsistencies in our definitions and in the resulting methods of thought.

Among scientists who are not biologists, biology has the reputation of being a very disorderly science. For example, Steele (1961, WADD, p. 488) stated "The engineer typically resents the sloppy amorphous quality of biological knowledge, its lack of precision, and its multivariate complexity." Steele also stated that "A man with a primary passion for synthesis or creative design simply does not become a biologist. The problems and attractions of biology are not those of synthesis and design, but of observation and analysis." A similar attitude is expressed by McCulloch (1961, WADD, p. 492) who stated "biology has by and large selected men who are good at observing, good at recording, and mathematically incompetent, unusually unable to think." Other comparable statements can be found in the literature.

I do not accept these statements at face value. Furthermore, I have no doubt that many other biologists will consider such statements as untrue, and if true, better unsaid, and if said, better not repeated. Some biologists may even agree that most other biologists are "unusually unable to think," and will automatically consider themselves to be excluded personally from McCulloch's statement by the phrase "by and large." However, much can be said to support the idea that biology is a disorderly subject.

We could expend much energy trying to defend our status as scientists, and many biologists will either deny that the ideas expressed above by Steele and by McCulloch are true or will accept them as facts and try to defend them as being necessary to the subject matter. However, I hope that others of us will try to remove whatever basis might exist for these statements, and the way to do that is to make biology more orderly. Superficially, taxonomy might appear to be the most orderly area of biology because it uses a neat outline for taxonomic groups. However, it seems to be one branch of biology in which much more order is needed, and also one in which more order can be attained by revision of a few fundamental concepts and by concentrated effort.

Since the above portion of this paper was written an article has appeared by Fein (1961) in which he predicts that by 1975 at least one botany department in a large university will offer a course in "The application of computer techniques to taxonomic botany." It is also possible that by 1975 the contents of such courses may be so well established in all of the life sciences that they no longer will be labeled "Applications to . . ." but simply "Taxonomic Botany," "Taxonomic Zoology," etc.

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Distribution and Establishment of a Land Isopod in North America

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THE LAND ISOPOD *Armadillidium nasatum* Budde-Lund, 1885 (=*quadrifons* Stoller, 1902) is a common European isopod found around human habitations and in greenhouses in moderate abundance (Waechtler, 1937). It ranges in Europe from Finland and Scandinavia to the Mediterranean (type locality: Rome). It was first recorded in the United States by Stoller (1902) who found it in a greenhouse in Schenectady, New York, and gave a complete description.

There has been much concern in the literature over the occurrence and degree of establishment of *A. nasatum* populations in North America but since most of the reports concern local populations only a general idea of the distribution of the species has been learned. No one has more than suggested that the species is permanently established in North America independent of immediate human influences. That the species can be an economic pest is well known (Hatch, 1947). One object of this study is to describe the range and general ecology of the species and to demonstrate that *A. nasatum* is not only established but well established and flourishing in North America in a region farther south than the localities from which it had previously been reported in the United States and Canada. Van Name (1936) states that the species in America is "apparently confined to hothouses and warmed buildings where, however, it may occur in abundance."

After Stoller's 1902 greenhouse record the species was found in Canadian greenhouses by Ross (1914) and Walker (1927). In the United States Longnecker (1924) found *A. nasatum* in a greenhouse in Mt. Pleasant, Iowa. Blake (1929, 1931) described *A. nasatum* from greenhouses in Cambridge, Massachusetts, and Middletown, Connecticut. Van Name (1936) adds to the early records "a storage warehouse in New York City" and later (1940) "under pieces of wood" in Glenview, Illinois, in October, 1936. Spencer (1942) records the species from British Columbia, Canada, and Smith and Goodhue (1945) found it in greenhouses in Beltsville, Maryland.

Hatch (1947) records many more greenhouse localities including New Jersey, Virginia, Kansas, and California. Some of Hatch's records, especially the more southern ones, although he does not say so, are most probably permanently established populations from outdoor localities. Hatchett (1947) and Hatch (1949) record *A. nasatum* from a greenhouse in Michigan and in Langley Prairie, British Columbia. Causey (1952, 1953), Eberly (1953), Muchmore (1957), and Cole (1959) record *A. nasatum* from what are probably established outdoor populations in localities in Arkansas, Indiana, New York State, and Kentucky, respectively.

In collections made from 1958 to 1961 *A. nasatum* was taken from Bethesda, Maryland, to Durham, North Carolina. In traveling south from Maryland through Virginia, *A. nasatum* increases in frequency in the collections, and, in the Durham region, more than a year of intensive collecting of isopods has demonstrated that it is the most abundant isopod to be found.

In Durham in the summer the species is found in almost every habitat favora-

ble to other isopod species, usually with *A. vulgare, Porcellio scaber, P. laevis, Cylisticus convexus,* and *Ligidium longicaudatum. A. nasatum* is usually the most abundant of the isopods where two or more species are found together, except in the very wettest or driest habitats. *A. nasatum* occurs in permanently wet areas around springs and on stream banks which are the natural habitats of *L. longicaudatum,* but it is never the most abundant species. In one habitat many *A. nasatum* were found at the waterline on rocks that were partially submerged in the water and mud of a small swamp. In the driest habitats, very close to buildings exposed to the sun most of the day and dry to the touch, many *A. vulgare,* but few *A. nasatum* were found. The *A. vulgare* were usually still and rolled into a ball, while the *A. nasatum* were active. *A. nasatum* is occasionally collected from rotten wood under the bark of deciduous trees in association with *Miktoniscus* sp.

In the autumn *A. nasatum* and other species congregate under the bark of trees or under boards and logs and remain in the protected spots throughout the winter. In summer *A. nasatum* was never found in conifer logs, but in winter as many as 1000 have been observed under the bark of pine logs. As many as 4000 isopods have been found crowded together in a suitable shelter (under an old railroad bridge tie by an outbuilding), and at least three-fourths of them were *A nasatum. Cylisticus convexus* is the most abundant associate of *A. nasatum* in the winter aggregations, if the habitat is around outbuildings near human habitation. If, however, the habitat is in the forest away from human influences *A. nasatum* is almost always found alone, or with less than one percent of *A. vulgare. Armadillidium vulgare* is always less numerous than *C. convexus* and the second most abundant associate of *A. nasatum* around human habitations.

Armadillidium nasatum is more or less active in the winter. It may be found on the underside of rocks and boards and even on the coldest days will roll into a ball if disturbed. The amount of winter activity depends upon the temperature of the habitat and inactivity on the coldest days is followed by moderate activity on warmer days. If all visible specimens in a given habitat are removed, more will be found a few weeks later, an indication of some winter displacement movements. Occasionally groups of animals were found dead in apparently unsuitable winter habitats. The activity of the animals increases in the spring and the tendency of disturbed individuals is to run rather than to roll into a ball. As the weather becomes warmer the animals of the winter aggregations disperse. In the Durham region aggregations are found from about mid-November until mid-March.

Muchmore (1957) states that in New York State the species was "lethargic but still alive" in cold weather, and suggests that it is found in permanent outdoor localities far from human habitations wherever suitable cold weather shelter exists. Muchmore found some specimens by a railroad and he states, "the animals are able to overwinter in these locations by burrowing deeply into the loose material of the railroad bed." Another group was found to "burrow deeply along the building foundations during the very cold weather." Many similar habitats occur in the Durham region and in the winter are usually occupied by *A. nasatum.*

According to Muchmore, the associates of *A. nasatum* in New York State were *C. convexus* and *Trachelipus rathkei.* The latter occurs with *A. nasatum* in Maryland and northern Virginia, but its range apparently does not extend as far south as North Carolina. *Trachelipus rathkei* is found abundantly within its range (Walker, 1927; Hatchett, 1947), and within the most northern part of its range it is the most abundant species, just as *A. nasatum* is the most abundant species in the Durham region north into Virginia. The lack of any large populations

of *A. nasatum* in the north suggests that there may be some interspecific competition between it and *T. rathkei* where their ranges overlap such as in New York State. There is probably a difference in ability to withstand cold between the two species also.

Armadillidium nasatum has a very long breeding season which extends over the whole summer, but is greater in the spring and early summer. In April 6.2% of the females were gravid and 61% were gravid in May. June was the month of peak reproductive activity, when 88.2% of the females were gravid. In July 66% of the females were gravid, and even in the months of August and September, several gravid females were found. Four months of relatively high reproductive activity, then, is characteristic of the females in the Durham area.

In addition to its ability to overwinter outdoors, the ecological advantages of *A. nasatum* over other isopods in the Durham region, especially over closely related *A. vulgare,* appear to be its longer breeding season and its capabilities of adapting to a wide range of environmental conditions. Although *A. nasatum* is not found in the very driest places in which *A. vulgare* may be found, nor in the very wettest places in which *L. longicaudatum* may be found, it does occur in the wide spectrum of wet-dry habitats between the extremes. It is not unusual for *A. nasatum* to be the most abundant species in any particular suitable habitat.

The spring breeding season of *A. nasatum* is longer than that of any other isopod which would be a direct competitor in the Durham region, and is about a month longer than that of *A. vulgare,* so even though *A. vulgare* females have a higher average number of young per spring brood (65.5 compared to 51 for *A. nasatum*), the number of *A. nasatum* young per female averages more per year because many *A. nasatum* females have a second brood later in the summer. In the Durham region at least, the species probably has the highest number of young per year of any isopod population.

It has been established in the preceding paragraphs that *A. nasatum* has been recorded from most of the northern part of the United States and southern Canada since it was first reported in 1902. It has never been thought to be well established in much of the northern range, but new records and a brief ecological study of the species in Durham, North Carolina, demonstrate beyond a doubt that it is one of the major species of isopods and permanently established in a part of the United States from which it has never before been recorded.

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Review

PRINCIPLES OF ANIMAL TAXONOMY. By George Gaylord Simpson. Columbia University Press, New York, 1961. 247 pp., $6.00.

It is very seldom that a taxonomist has an opportunity to review a book which is certain to have a wide influence among students of all groups of organisms, living and fossil. If the book also clarifies the taxonomists' problems in larger measure than it aggravates them, the opportunity is doubly rare. If the book happens to be written in language of unusual clarity, with few of the unjustified statements so commonly used in textbooks, the event assumes a unique position.

Zoologists who notice the difference between a glib generalization couched in careless phraseology employing misleading words and a careful statement based on clear thought and reasoned premises will welcome another book from the hand and mind of the clearest writer in this field in our time. It is not necessary to agree with Simpson, but it is hard to misunderstand him. This makes discussion of disagreements easy and effective and leads to further clarification of ideas.

By "taxonomy" Simpson means the theoretical study of the basis, principles, procedures, and rules of classification. Many people who think of themselves as taxonomists will find that they have little in common with this study of the concepts but instead are concerned with the study of the kinds and diversity of organisms, which is systematics as defined here. The book actually deals with a good deal of systematics and might have been better described by the less attractive title of *Basis and Concepts of Systematics.*

Six chapters cover the background, nature, basis, and concepts of classification. Chapter 1 gives the clear definitions on which the entire discussion is based. Chapter 2 outlines the development of modern taxonomy. Chapter 3 discusses the evidence on which classifications are based and some of the implications of evolutionary theory to taxonomy. Chapter 4 discusses the mechanics of classification under such headings as objectivity, polyphyly, splitting and lumping, and relative antiquity. Chapter 5 discusses several kinds of species, infraspecific variation, and types. Chapter 6 is about higher categories.

Conceptually, this book is an outgrowth of the essay on classification published in 1945 in Simpson's classic paper *The Principles of Classification and a Classification of Mammals.* It bears little resemblance to that essay, however, and faces many problems not mentioned at that time. The entire story has become more unified, but it has thereby also become more dependent upon basic assumptions. Simpson has changed his mind about some things, after more study, and has assembled and analyzed the ideas of many other workers.

The background theme of the book, essential to most of its arguments, is the evolutionary basis of animal variation and classification. "The principles of modern taxonomy are evolutionary and the approach to classification here taken is correspondingly evolutionary or in a somewhat special sense phylogenetic." It is assumed as the basis for the entire book that no one ever classifies individual animals, specimens, but only populations; that the classifier draws from the populations some inferences as to their evolutionary pattern and then translates these conclusions into groups in a hierarchy; and that there are adequate criteria available for inferring this phylogeny.

The subject matter appropriate to such

a book is extremely varied. As a result no clear arrangement is evident such as would make it a gradual introduction to a casual reader, leading from simple ideas to more complex or esoteric ones. Some rather brief references, to concepts like set theory, the scholastic terminology of Aristotle and Aquinas, the historical development of ideas which are useful to us only in their modern form, seem out of place in the sense of being too technical for introductory readers and not presented in sufficient detail for an advanced student. Although this book is unquestionably deserving of wide study among workers and students alike, there is some question of whether it can readily be adapted to reading and discussion in classes. (The reviewer intends to try such use in an advanced taxonomy course.)

A large number of ideas are discussed. Many are dealt with in more detail than in most other modern books. These discussions will be valuable for their clarification of the problems. Whether or not they actually solve the problems will depend on whether the reader accepts the premises involved. This reviewer does not wish to single out statements with which he agrees or disagrees, although discussion of some of these points is already in press elsewhere, written before this book was announced, but it will be of interest to point out some of the controversial subjects on which Simpson presents his analysis. These are so numerous that they can be cited only very briefly.

In the first place, definitions are given for systematics, classification, nomenclature, taxonomy, hierarchy, key, taxon, category, homology, parallelism, convergence, mimicry, monophyly, evolutionary species, etc. These definitions are clear and explicit, giving basis for the discussions. They also leave room for individual disagreement, each of which may lead to a denial of dependent conclusions. For example, the type system is described at some length with the use of the now common terms archetype, typology, morphotype, and essence. These terms are common only in the recent literature of evolutionary taxonomy, where they are almost invariably used as descriptive of "The Old Systematics" in a derogatory tone. The terms are entirely meaningless to many working taxonomists, who frequently do not even understand the discussion of them. The implication that the bulk of taxonomic study consciously uses these concepts is entirely unjustified.

A viewpoint undoubtedly related to this, and very likely the basis for continued attack on the use of types, is the idea that populations are the basis of classification: "Modern taxonomic practice, concerned with *populations* and not *types* . . . " "Populations, not individuals, are the units of systematics and are the things classified." In practice, many taxonomists are entirely without knowledge of any populations. Their "samples" are generally too small to be of any use in conceiving the population. There is no fixed minimum sample size adequate to represent a species, as Kinsey learned when a collection of 40,000 specimens proved to be inadequate. Taxonomists would often like to know the nature of the population and the ranges of species characteristics, but they must and do work, in many cases if not most, with nothing but a few individuals. (The majority of all animal species are still known from one or a few specimens only.)

It is certain that the use of "paratype" by workers in different groups varies considerably. The supposition that it has always been used to show variation within the species is based on lack of experience in the larger groups. It is doubtful if nomenclaturists would agree that "Nomenclature requires and indeed can tolerate no type but *the* type or holotype." inasmuch as several others are officially recognized and almost universally used. Whatever the theoretical soundness of Simpson's ideas on this, they do not correspond with practice in taxonomy in general. Nor is his belief in current employment of archetypes justified in the field as a whole.

Many taxonomists have found them-

selves outside of *The New Systematics*, because their fields are simply not advanced to the point of using the concepts that are required by definition. These taxonomists will be interested to know that they may be barred from ever practicing modern taxonomy, because "Modern taxonomic practice . . . requires as far as possible series of specimens large enough for inference as to the total variation in the population from which the sample is drawn." Such large samples are available very rarely in taxonomy as a whole and are entirely lacking in many groups of animals.

The vertebrate viewpoint applied to all animals appears again in the discussion of subspecies. We find the statement that most species obviously do have distinguishable geographic subgroups. This is not limited to higher vertebrates or better known groups. As a general statement it will be seen to be far too sweeping, as a large number of species in most phyla are known insufficiently for any geographic analysis. Some taxonomists may believe that the statement will eventually be found to be applicable to all groups, but that is a long way in the future.

Here is also one of the rare cases in this book in which an entirely unjustified—and unjustifiable—statement appears: "The vast majority of modern taxonomists agree . . ." It makes no difference how this sentence ends—there is no way that anyone can know the views of all taxonomists on any question. There is no way to know even who are the "modern" taxonomists, unless we define the modern ones as those who do agree. This would make the whole statement a specious circular argument.

Some taxonomists have concerned themselves with whether or not the groups they segregate are monophyletic. If they have examined the general problem of polyphyly in much detail, they will know that polyphyly does not mean the same thing to all workers. To some it means that every species in an order evolved from one pair of ancestral individuals. To others it means merely that all species in an order evolved from the various species of some ancestral order—many parallel lineages. Simpson adopts the latter view, as do other vertebrate paleontologists.

A considerable discussion of "splitting and lumping" brings out the difference in extreme viewpoint at the level of genera. This discussion is so closely tied to phylogenetic ideas that it is almost useless to one who classifies without direct reference to phylogeny. It brings out the important factor of the personality of the worker but seems to deal inadequately with the extreme variation in size of groups as they occur at the present time in nature. It implies that there can be a standard "balance" between monotypic groups and others, whereas some taxonomists will hold that some invertebrate groups seem to show a very high ratio of monotypic groups while others show a very low ratio.

Simpson believes firmly that homology is the basis of classification because it is the result of phylogeny. He discusses the criteria of homology, but it is difficult to find in his discussion any real basis on which decisions can be made on homology. This seems to leave us just where we have always been—we believe homology is important, we may believe it is important because it results from phylogeny, but we have no basis except personal judgment to decide whether it exists in any given case.

The concept of species as groups of actually or potentially interbreeding populations is now familiar to most taxonomists. Simpson states that "In most groups of recent animals it is both applicable and sufficient," and "an experienced taxonomist can apply it with little difficulty to probably at least nine-tenths, perhaps even more, of animals to be classified." This would seem to mean that the thousands of kinds of non-interbreeding animals cannot be classified at all. Even in the cases where interbreeding criteria are theoretically obtainable, they are ac-

tually available to taxonomists in only a minute percentage of kinds.

It has been customary for paleontologists to consider themselves geologists rather than biologists. It is doubtful if Simpson adopts this view. Nevertheless, he emphasizes supposed differences between paleontology and neontology, as follows: "The data for classification of fossils are characteristically different from those in neontology and present many special problems." The six problems cited will be recognized by many neontologists as being substantially applicable to their groups of living animals also. It is difficult to see any real difference, except if one's view is primarily that of a specialist on vertebrates.

Any taxonomist who has thought at all about the basis of his studies will find other ideas with which he may disagree. This provocation of further thought will be the major contribution of this book, made effective by clear definitions. The vertebrate-slanted viewpoint is clearly recognizable and can be discounted in other fields. It is the fault of invertebrate workers that the inapplicability of many of these ideas to their part of the animal kingdom is not widely understood.

One danger will remain. It has already happened once in taxonomy in our generation that a book of importance in *stimulating thought and discussion* was accepted by many as being authoritative, as giving the final indisputable position on certain aspects of taxonomy. Simpson's book comes much closer to fulfilling this lofty goal, but it would be a mistake even here to believe that there is any final word on these problems. Simpson would be the first to agree that contrary views exist and can also be supported with logic and experience.

This reviewer hopes that it will be understood that criticisms implied here or differences of opinion suggested could probably be effectively answered by Simpson if he had an opportunity to do so. Really fundamental differences of opinion are not as common in this field as sometimes appears. It is intended merely to show some of the issues on which further thought, discussion, and clarification of terms would be useful.

It is a pleasure to recommend this book for thoughtful study by all zoologists who are interested in the systematization of knowledge and to all taxonomists who think about the basis and background of their work.

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